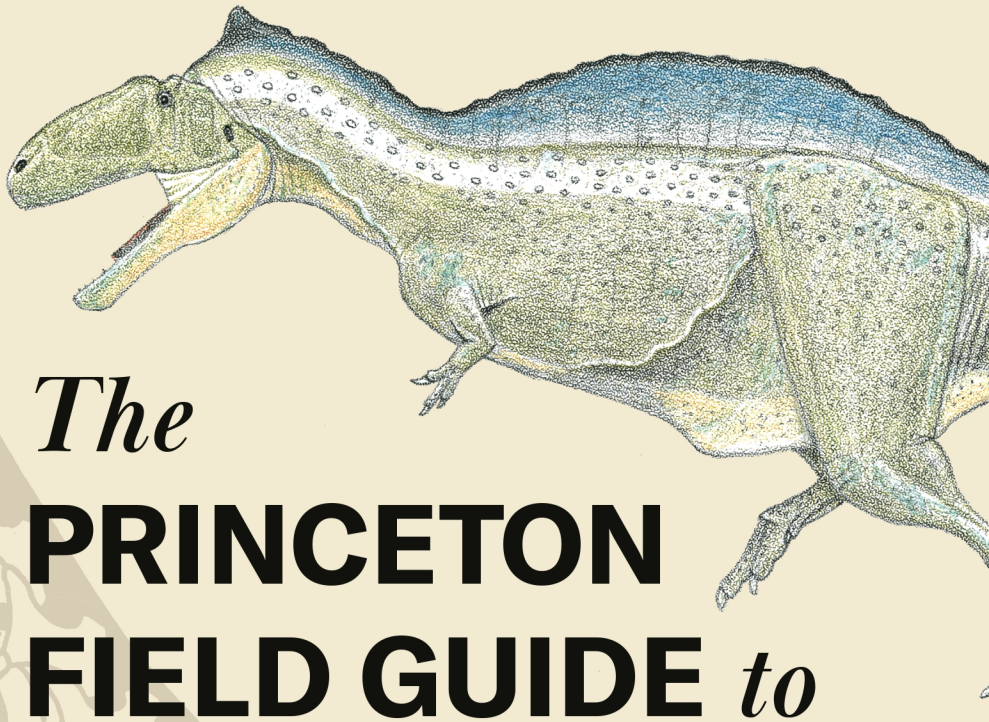
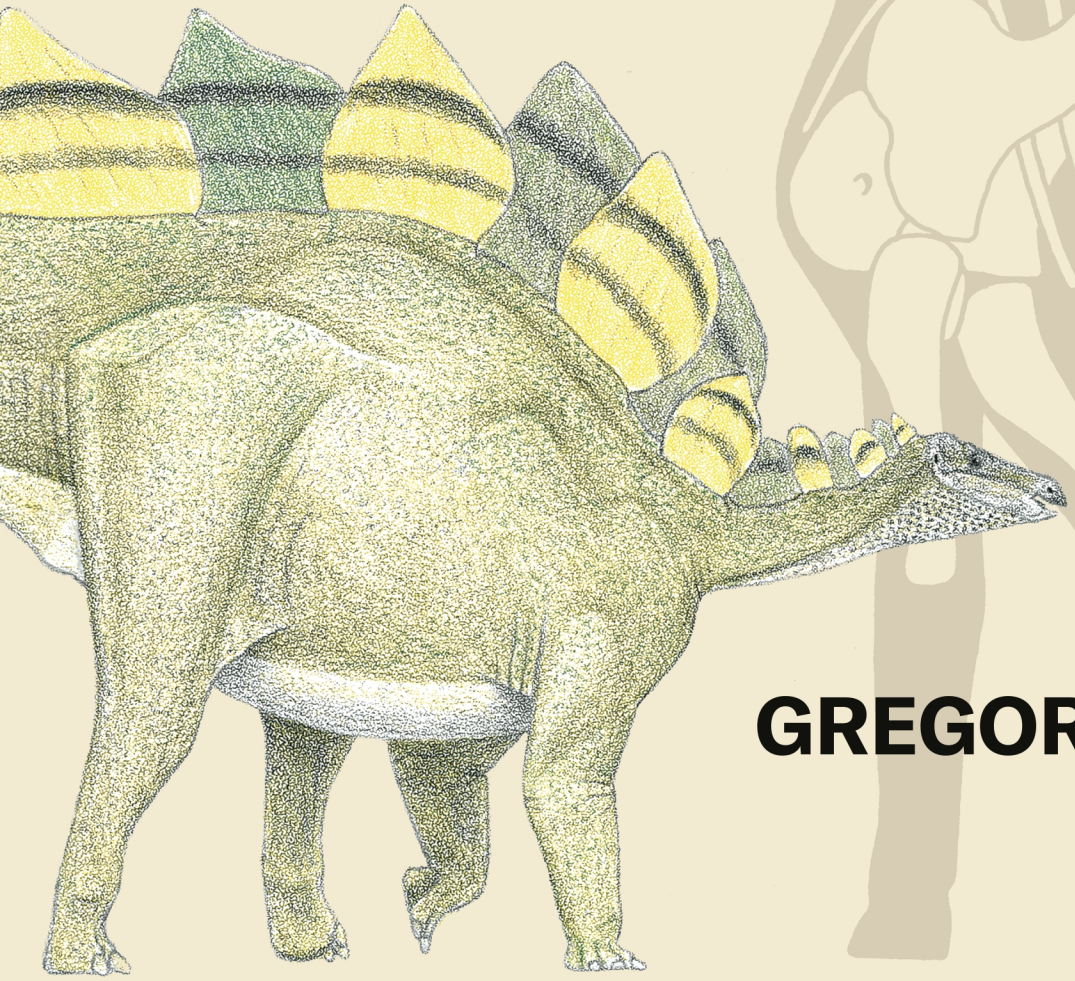


The PRINCETON FIELD GUIDE *to* DINOSAURS

3RD EDITION



GREGORY S. PAUL

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3RD EDITION

GREGORY S. PAUL

Princeton University Press
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PREFACE

If I were, at about age twenty as a budding paleozoologist and paleoartist, handed a copy of this book by a mysterious time traveler, I would have been shocked as well as delighted. The pages would reveal a world of new dinosaurs and ideas that I barely had a hint of or had no idea existed at all. My head would spin at the revelation of the therizinosaurs such as the wacky feathered *Beipiaosaurus* and at the biplane flying dromaeosaurids, not to mention the little halszkaraptors with their duck-like beaks, or the oversized shoulder spines of *Gigantspinosaurus*, the neck spines of *Amargasaurus*, the brow horns and atrophied arms of bulldog-faced *Carnotaurus*, the furry adornments of *Tianyulong* and *Kulindadromeus*, the bristly tail of *Psittacosaurus*, the extraordinary preservation of the armor of *Borealopelta*, the bat-like membranous wings of scansoriopterygids, the long-necked stegosaur *Miragaia*, and the often psychedelic frilled horns of the new stable of centrosaurine and chasmosaurine ceratopsids. Even *Triceratops* has proven to have strange skin. How about colossal new sauropods that gave the giant baleen whales a run for their money in terms of sheer bulk and could feed over six stories high in tree crowns? It is a particular pleasure to restore the skeleton of the once mysterious *Deinocheirus*, long known from only its colossal arms—its peculiar skeleton does not disappoint. And who would have imagined it would become possible to figure out the colors of some feathered dinosaurs? I would note the new names for some old dinosaurs, including my favorite, *Giraffatitan*. And that old *Brontosaurus* is back! And now there are three royal species of *Tyrannosaurus*: *T. rex*, *T. regina*, and *T. imperator*. There would be the dinosaur-bearing beds with the familiar yet often exotic names: Tendaguru, Morrison, Chinle, Wessex, Wealden, Lameta, Oldman, Kota, Kirtland, Arundel, Djadokhta, Nemegt, Cloverly, Navajo Sandstone, North Horn, Hell Creek, Portland, Lufeng, Arundel, New Egypt, Lance. Plus there are the novel formations, at least to my eyes and ears: Yixian-Jiufotang, Tiourarén, Dinosaur Park, Eumeralla, Longjiang, Two Medicine, Anacleto, Painten, Shishugou, Huincul, Aguja, Ischigualasto, Qingshan, Cerro del Pueblo, Hanson, Jinhua, Clearwater, Tiaojishan, Tsagayan, Tropic Shale, Mackunda, Blackleaf, Pari Aike, Ukureyskaya, Villar del Arzobispo, Tegana, Kallamedu, Wapiti, Bungil, Demopolis, Portezuelo, Prince Creek, Ulansuhai, Ulaanoosh, Sânpetru, Shinekhudag, Kitadani, Zhanghe, Woodbine, Calizas de la Huérguina, Chaochuan, Xert, Maevarano. The sheer number of new dinosaurs would demonstrate that an explosion in dinosaur discoveries and research, far beyond anything that had previously occurred, and often based on new high technologies, marked the end of the twentieth century going into the twenty-first.

Confirmed would be the paradigm shift already under way in the late 1960s and especially the 1970s that observed that dinosaurs were not so much reptiles as they were near birds that often paralleled mammals in form and function. Dinosaurs were still widely seen as living in tropical swamps, but we now know that some lived through polar winters so dark and bitterly cold that low-energy reptiles could not survive. Imagine a small dinosaur shaking the snow off its hairy body insulation while the flakes melt on the scaly skin of a nearby titanic dinosaur whose body, oxygenated by a birdlike respiratory complex and powered by a high-pressure four-chambered heart, produces the heat needed to prevent frostbite.

In just the eight years since the appearance of the second edition of this book, the number of dinosaur species named has expanded about 15 percent relative to some 200 years of research—if anything, there was more updating between this edition and the second than between that and the first. Producing this third edition has been satisfying in that it has given me yet more reason to more fully achieve a long-term goal, to illustrate the skeletons of almost all dinosaur species for which sufficiently complete material is available. These have been used to construct the most extensive library of side-view life studies of dinosaurs in print to date. The result is a work that covers what is now two centuries of scientific investigation into the group of animals that ruled the continents for over 150 million years. Enjoy the travel back in time.

ACKNOWLEDGMENTS

A complaint earlier this century on the online Dinosaur List by Ian Paulsen about the absence of a high-quality dinosaur field guide led to the production of the first and then the second edition of this dinosaur guide. The exceptional success of those editions combined with the continuous flux of new discoveries and research led to production of a third. Many thanks to those who have provided the assistance over the years that has made this book possible, including Kenneth Carpenter, Asier Larramendi, Michael Brett-Surman, Philip Currie, John McIntosh, Robert Bakker, Peter Galton, James Kirkland, Scott Persons, Rinchen Barsbold, John Horner, Xu Xing, Frank Boothman, Daniel Chure, David Burnham, Kristina Curry Rogers, Alex Downs, Steven and Sylvia Czerkas, Peter Dodson, David Evans, James Farlow, Jay Van Raalte, Hermann Jaeger, Frances James, Tracy Ford, Catherine Forster, Rodolfo Coria, John Foster, Mike Fredericks, Roland Gangloff, Donald Glut, Mark Hallett, Jerry Harris, Thomas Holtz,

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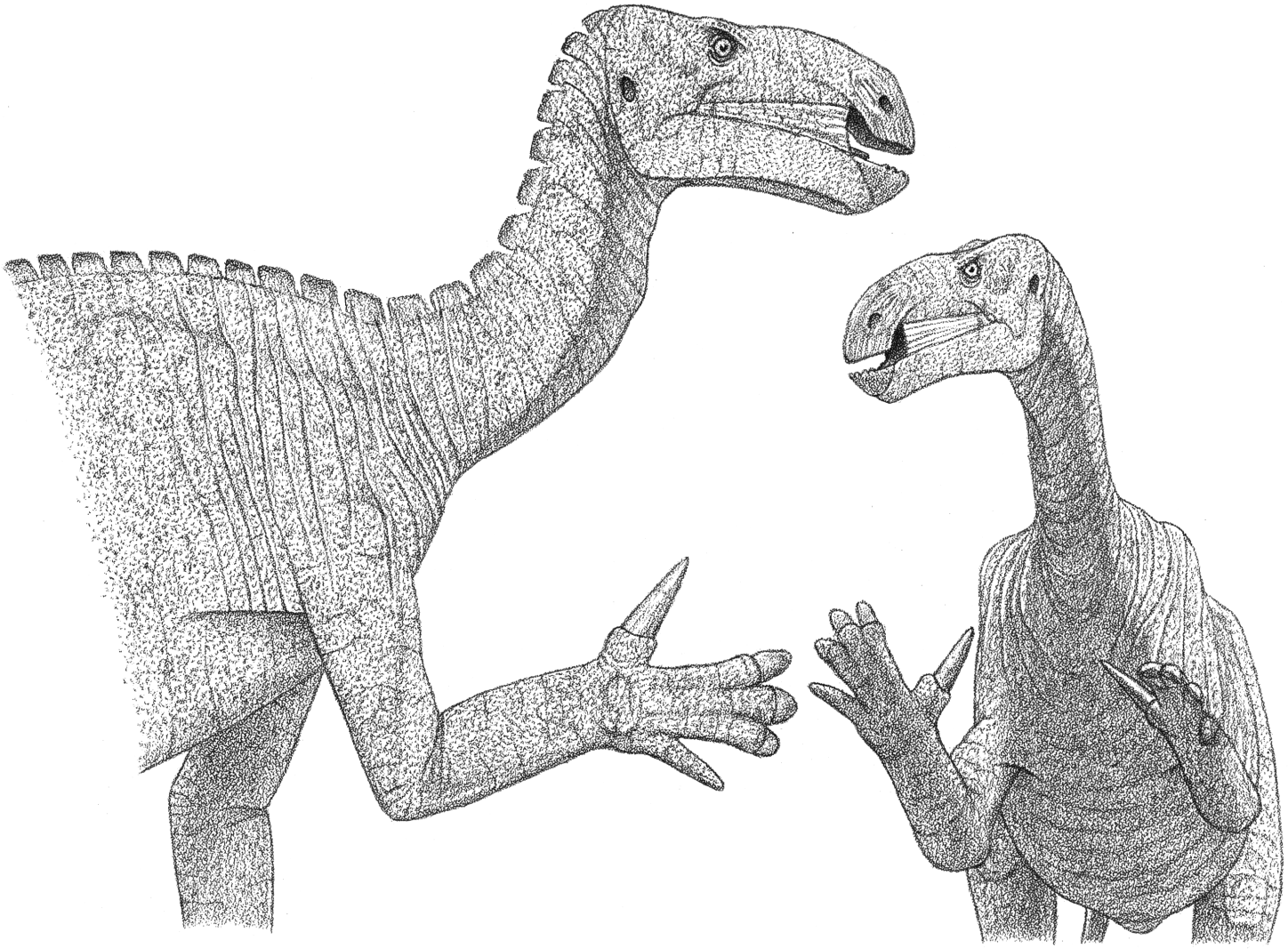
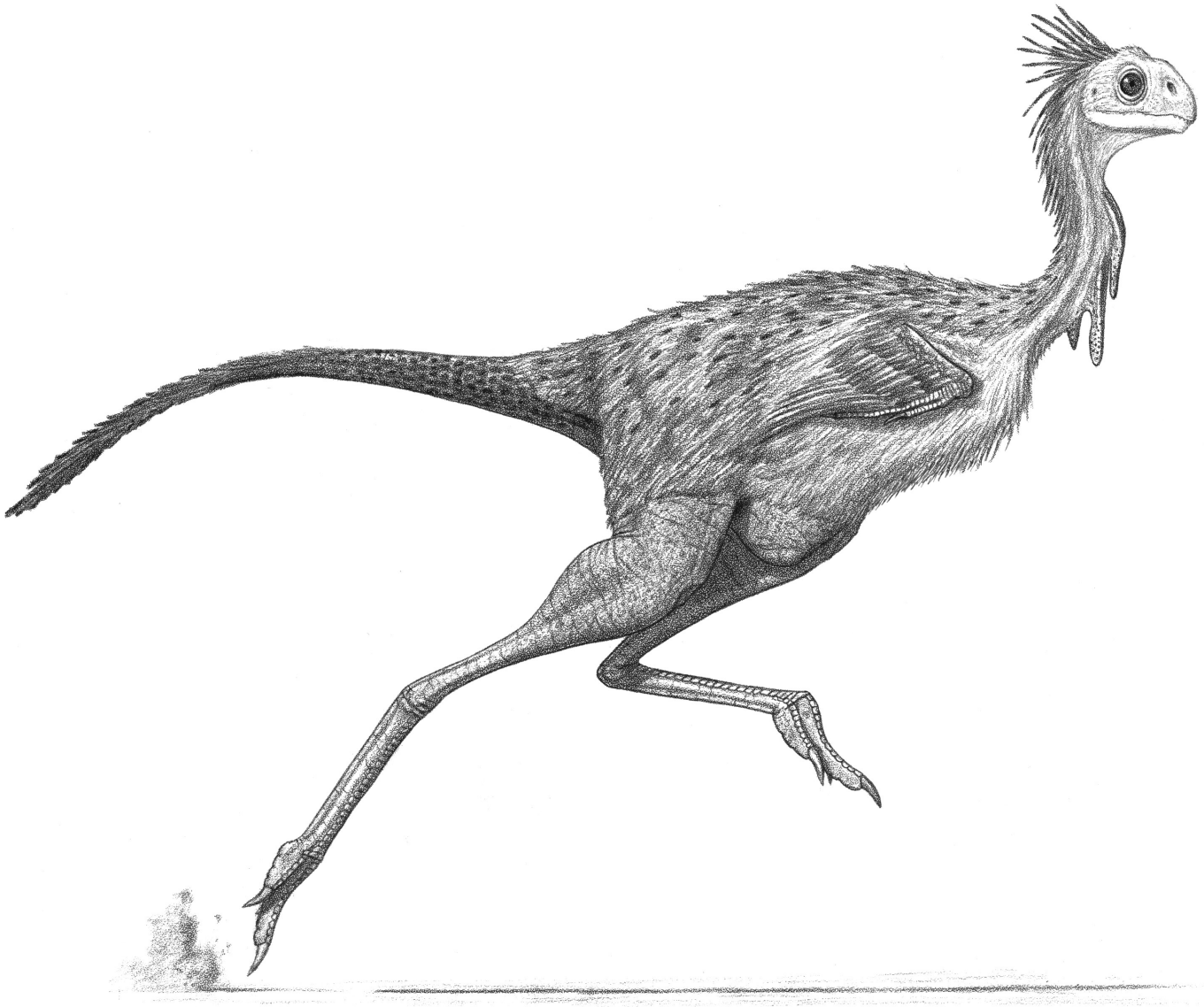


Iguanodon



The feathery dinosaur *Avimimus*

INTRODUCTION

HISTORY OF DISCOVERY AND RESEARCH

Dinosaur remains have been found by humans for millennia and probably helped form the basis for belief in mythical beasts including dragons. A few dinosaur bones were illustrated in old European publications without their true nature being realized. In the West the claim in the Genesis creation story that the planet and all life were formed just two thousand years before the pyramids were built hindered the scientific study of fossils. At the beginning of the 1800s the numerous three-toed trackways found in New England were attributed to big birds, in part because they lacked tail drag marks. By the early 1800s the growing geological evidence that Earth's history was much more complex and extended back into deep time began to free researchers to consider the possibility that long-extinct and exotic animals once walked the globe.

Modern dinosaur paleontology began in the 1820s in England. Teeth were found, and a few bones of the predatory *Megalosaurus* and herbivorous *Iguanodon* were published and named in 1824 and 1825. For a few decades it was thought that the bones coming out of ancient sediments were the remains of oversized versions of modern reptiles. In 1842 Richard Owen recognized that many of the fossils were not standard reptiles, and he coined the term "Dinosauria" to accommodate them. Owen had preevolutionary concepts of the development of life, and he envisioned dinosaurs as elephantine versions of reptiles, so they were restored as heavy-limbed quadrupeds. This led to the first full-size dinosaur sculptures for the grounds of the Crystal Palace in the 1850s, which helped initiate the first wave of dinomania as they excited the public. A banquet was actually held within one of the uncompleted figures. These marvelous examples of early dinosaur art still exist.

The first complete dinosaur skeletons, uncovered in Europe shortly before the American Civil War, were those of small examples, the armored *Scelidosaurus* and the birdlike *Compsognathus*. The modest size of these fossils limited the excitement they generated among the public. Found shortly afterward in the same Late Jurassic Solnhofen sediments as the latter was the "first bird," *Archaeopteryx*, complete with teeth and feathers. The remarkable mixture of avian and reptilian features preserved in this little dinobird did generate widespread interest, all the more so because the publication of Charles Darwin's theory of evolution at about the same time allowed researchers to put these dinosaurs in a more proper scientific context. The enthusiastic advocate of biological evolution Thomas Huxley argued that the close similarities between *Compsognathus* and *Archaeopteryx* indicated a close link between the two groups. In the late 1870s Belgian coal miners came across the complete skeletons of iguanodonts that confirmed that they were long-legged, three-toed semibipeds, not full quadrupeds.

At this time, the action was shifting to the United States. Before the Civil War, incomplete remains had been found on the Eastern Seaboard. But matters really got moving when it was realized that the forest-free tracts of the West just being cleared of the First Peoples offered hunting grounds that were the best yet for the fossils of extinct titans. This quickly led to the "bone wars" of the 1870s and 1880s in which Edward Cope and Charles Marsh, having taken a dislike for one another that was as petty as it was intense, engaged in a bitter and productive competition for dinosaur fossils that would produce an array of complete skeletons. For the first time it became possible to appreciate the form of classic Late Jurassic Morrison dinosaurs such as agile predatory *Allosaurus* and *Ceratosaurus*, along with *Apatosaurus*, *Brontosaurus*, *Diplodocus*, and *Camarasaurus*—which were really elephantine quadrupeds—the protoiguanodont *Camptosaurus*, and the bizarre plated *Stegosaurus*. Popular interest in the wonderful beasts was further boosted.

By the turn of the century, discoveries shifted to younger deposits such as the Lance and Hell Creek, which produced classic dinosaurs from the end of the dinosaur era including duck-billed *Edmontosaurus*, armored *Ankylosaurus*, horned *Triceratops*, and the great *Tyrannosaurus*. As paleontologists moved north into Canada in the early decades of the twentieth century, they uncovered a rich collection of slightly older Late Cretaceous dinosaurs including *Albertosaurus*, horned *Centrosaurus*, spiked *Styracosaurus*, and the crested duckbills *Corythosaurus* and *Lambeosaurus*.

Inspired in part by the American discoveries, paleontologists in other parts of the world looked for new dinosaurs. Back in Europe abundant skeletons of German *Plateosaurus* opened a window into the evolution of early dinosaurs in the Late Triassic. In southeastern Africa the colonial Germans uncovered at exotic Tendaguru the supersauropod *Giraffatitan* (was *Brachiosaurus*) and spiny *Kentrosaurus*. In the 1920s Henry Osborn at the American Museum in New York dispatched Roy Andrews to Mongolia in a misguided search for early non-African humans that fortuitously led to the recovery of small Late Cretaceous dinosaurs, parrot-beaked *Protoceratops*, the "egg-stealing" *Oviraptor*, and the advanced, near-bird theropod *Velociraptor*. Dinosaur eggs and entire nests were found, only to be errantly assigned to *Protoceratops* rather than the oviraptorid that had actually laid and incubated them. As it happened, the Mongolian expeditions were somewhat misdirected. Had paleontologists

also headed northeast of Beijing, they might have made even more fantastic discoveries that would have dramatically altered our view and understanding of dinosaurs, birds, and their evolution, but that event would have to wait another three-quarters of a century.

The mistake of the American Museum expeditions in heading northeast contributed to a set of problems that seriously damaged dinosaur paleontology as a science between the twentieth-century world wars. Dinosaurology became rather ossified, with the extinct beasts widely portrayed as sluggish, dim-witted evolutionary dead ends doomed to extinction, an example of the "racial senescence" theory that was widely held among researchers who preferred a progressive concept of evolution at odds with more random Darwinian natural selection. It did not help matters when artist-paleontologist Gerhard Heilmann published a seminal work that concluded that birds were not close relatives of dinosaurs, in part because he thought dinosaurs lacked a wishbone furcula, which had just been found, but misidentified, in *Oviraptor*. The advent of the Depression, followed by the trauma of World War II—which led to the loss of some important fossils on the continent as a result of Allied and Axis bombing—brought major dinosaur research to a near halt.

Even so, public interest in dinosaurs remained high. The paleoart of Charles Knight made him famous. The *Star Wars–Jurassic Park* of its time, RKO's *King Kong* of 1933 amazed audiences with its dinosaurs seemingly brought to life. Two major film comedies, 1938's *Bringing Up Baby*, starring Cary Grant and Katherine Hepburn, and 1949's *On the Town*, featuring Gene Kelly and Frank Sinatra, involved climactic scenes in which sauropod skeletons at a semifictional New York museum collapsed because of the hijinks of the lead characters. Unfortunately, the very popularity of dinosaurs gave them a circus air that convinced many scientists that they were beneath their scientific dignity and attention.

Despite the problems, discoveries continued. In an achievement remarkable for a nation ravaged by the Great Patriotic War and suffering under the oppression of Stalinism, the Soviets mounted postwar expeditions to Mongolia that uncovered the Asian version of *Tyrannosaurus*, a.k.a. *Tarbosaurus*, and the enigmatic arms of enormous clawed *Therizinosaurus*. Equally outstanding was how the Poles, led by the renowned Halszka Osmólska, took the place of the Soviets in the 1960s, discovering in the process the famed complete skeleton of *Velociraptor* engaged in combat with *Protoceratops*. They too found another set of mysterious long arms with oversized claws, *Deinocheirus*. Another leader of Mongolian paleozoology has been the native Rinchen Barsbold.

In the United States, Roland Bird studied the trackways of herds of Texas-sized Cretaceous sauropods before World War II. Shortly after the global conflict, the Triassic Ghost Ranch quarry in the Southwest, packed with complete skeletons of little *Coelophysis*, provided the first solid knowledge of the beginnings of predatory dinosaurs. Also found shortly afterward in the Southwest was the closely related but much larger crested theropod *Dilophosaurus* of the Early Jurassic.

What really spurred the science of dinosaur research were the Yale expeditions to Montana in the early 1960s that dug into the little-investigated Early Cretaceous Cloverly Formation. The discovery of the *Velociraptor* relative *Deinonychus* finally made it clear that some dinosaurs were sophisticated, energetic, agile dinobirds, a point reinforced by the realization that they and the other sickle claws, the troodontids, as well as the ostrichlike ornithomimids, had fairly large, complex brains. These developments led John Ostrom to note and detail the similarities between his *Deinonychus* and *Archaeopteryx* and to conclude that birds are the descendants of energetic small theropod dinosaurs. Ostrom further observed that the bird- and mammal-like body design of dinosaurs meant that that their newly apparent presence in Arctic regions could not be taken as evidence that those ancient polar habitats were warm even in winter.

Realizing that the consensus dating back to the original discovery that dinosaurs were an expression of the reptilian pattern was flawed, Robert Bakker in the 1960s and 1970s issued a series of papers contending that dinosaurs and their feathered descendants constituted a distinct group of archosaurs whose biology and energetics were more avian than reptilian. In the eye-popping article "Dinosaur Renaissance" in a 1975 *Scientific American*, Bakker proposed that some small dinosaurs themselves were feathered. In the late 1970s, Montana native John Horner found baby hadrosaurs and their nests, providing the first look at how some dinosaurs reproduced. At the same time, researchers from outside paleontology stepped into the field and built up the evidence that the impact of a mountain-sized asteroid was the long-sought great dinosaur killer. This extremely controversial and contentious idea turned into the modern paradigm when a state-sized meteorite crater was found in southeastern Mexico dating to the end of the dinosaur era. At the same time, the volcanic Deccan Traps of India were proposed as an adjunct in the demise of the nonbird dinosaurs.

These radical and controversial concepts greatly boosted popular attention on dinosaurs, culminating in the *Jurassic Park* novels and films that sent dinomania to unprecedented heights. The elevated public awareness was combined with digital technology in the form of touring exhibits of robotic dinosaurs. This time the interest of paleontologists was raised as well, inspiring the second and ongoing golden age of dinosaur discovery and research, which is surpassing that which has gone before. Assisting the work are improved scientific techniques in the area of evolution and phylogenetics, including cladistic genealogical analysis, which has improved the investigation of dinosaur relationships. New generations of artists have portrayed dinosaurs with a "new look" that lifts tails in the air and gets feet off the ground to represent the more dynamic gaits that are in

Deinonychus and *Tenontosaurus*

line with the more active lifestyles the researchers now favor. This artist and researcher noticed that the sickle-clawed dromaeosaurs and troodonts, as well as the oviraptorosaurs, possessed anatomical features otherwise found in flightless birds and suggested that these dinosaurs were also secondarily flightless.

Dinosaurs are being found and named at an unprecedented rate as dinosaur science goes global, with efforts under way on all continents. In the 1970s the annual Society of Vertebrate Paleontology meeting might have seen a half-dozen presentations on dinosaurs; now it is in the area of a couple of hundred. Especially important has been the development of local expertise made possible by the rising economies of many second-world nations, reducing the need to import Western expertise.

In South America, Argentine and American paleontologists collaborated in the 1960s and 1970s to reveal the first Middle and Late Triassic protodinosaurs, finally showing that the very beginnings of dinosaurs started among surprisingly small archosaurs. Since then, Argentina has been the source of endless remains from the Triassic to the end of the Cretaceous that include the early dinosaurs *Eoraptor* and *Herrerasaurus*, supertitanosaur sauropods such as *Argentinosaurus*, *Futalognkosaurus*, and *Dreadnoughtus*, and oversized theropods such as *Giganotosaurus* that preyed on them. Among the most extraordinary finds have been sauropod

nesting grounds that allow us to see how the greatest land animals of Earth's history reproduced themselves.

In southern Africa excellent remains of an Early Jurassic species of *Coelophysis* verified how uniform the dinosaur fauna was when all continents were gathered into Pangaea. Northern Africa has been the major center of activity as a host of sauropods and theropods have filled in major gaps in dinosaur history. Australia is geologically the most stable of continents, with relatively little in the way of tectonically driven erosion to either bury fossils or later expose them, so dinosaur finds have been comparatively scarce despite the aridity of the continent. The most important discoveries have been of Cretaceous dinosaurs that lived close to the South Pole, showing the climatic extremes dinosaurs were able to adapt to. Glacier-covered Antarctica is even less suitable prospecting territory, but even it has produced the Early Jurassic crested avepod *Cryolophosaurus* as well as other dinosaur bones.

At the opposite end of the planet, the uncovering of a rich Late Cretaceous fauna on the Alaskan North Slope confirms the ability of dinosaurs to dwell in latitudes cold and dark enough in the winter that lizards and crocodilians are not found in the same deposits. Farther south, a cadre of researchers have continued to plumb the great dinosaur deposits of western North America as they build the most detailed sample of dinosaur evolution from the Triassic until their final loss. We now know that armored ankylosaurs were roaming along with plated stegosaurs in the Morrison Formation, a collection of sauropods has been exposed from the Early Cretaceous, and one new ceratopsian and hadrosaur and theropod and ankylosaur after another is coming to light in the classic Late Cretaceous beds.

Now Mongolia and especially China have become a great frontier in dinosaur paleontology. Even during the chaos of the Cultural Revolution, Chinese paleontologists made major discoveries, including the first spectacularly long-necked mamenchisaur sauropods. As China modernized and Mongolia gained independence, Canadian and American researchers worked with their increasingly skilled and independent resident scientists, who have become a leading force in dinosaur research. It was finally realized that the oviraptors found associated with nests at the Flaming Cliffs were not eating the eggs but brooding them in a preavian manner. Almost all of China is productive when it comes to dinosaurs, and after many decades paleontologists started paying attention to the extraordinary fossils being dug up by local farmers from Early Cretaceous Yixian-Jiufotang lake beds in the northeast of the nation.

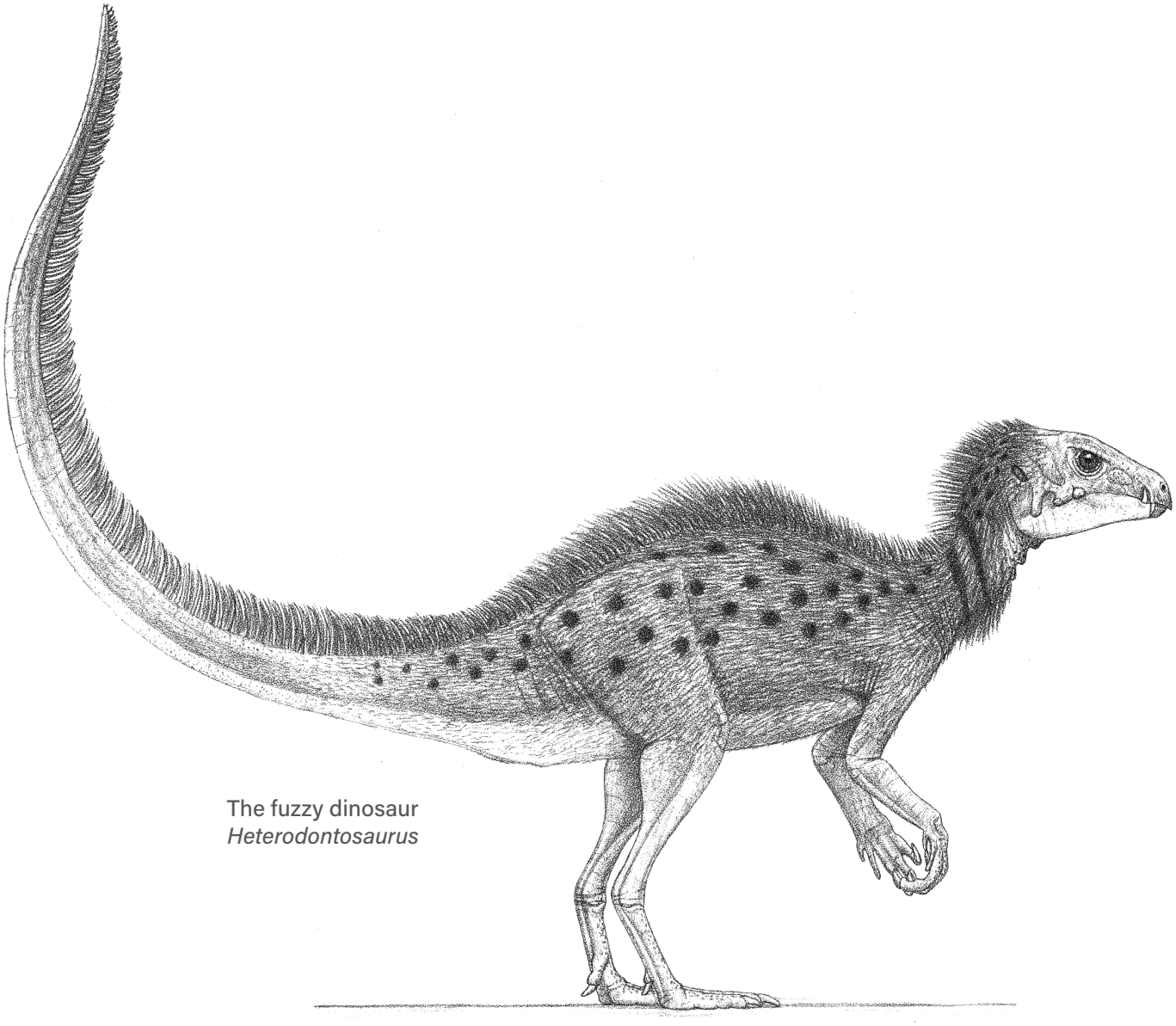
In the mid-1990s, complete fossils of small compsognathid theropods labeled *Sinosauropteryx* began to show up with their bodies covered with dense coats of bristly protofeathers, to the delight of Ostrom and others. More recently it has been argued that it is often possible to determine the color of the feathers! This was just the start: the Yixian-Jiufotang beds are so extensive and productive that they have become an inexhaustible source of beautifully preserved material as well as of strife, as the locals contend with the authorities for the privilege of excavating the fossils for profit—sometimes altering the remains to "improve" them—rather than for rigorous science. The feathered dinosaurs soon included the potential oviraptorosaur *Caudipteryx*. Even more astonishing have been the Yixian-Jiufotang dromaeosaurs. These small sickle claws bear fully developed wings not only on their arms but on their similarly long legs as well. This indicates not only that dromaeosaurs first evolved as fliers but that they were adapted to fly in a manner quite different from the avian norm. The therizinosaur *Beipiaosaurus* looks like a refugee from a Warner Brothers cartoon. But the Yixian-Jiufotang is not just about confirming that birds are dinosaurs and that some dinosaurs were feathered. One of the most common dinosaurs of the Early Cretaceous was the parrot-beaked *Psittacosaurus*. Although it was known from numerous skeletons across Asia found over the last eighty years, no one had a clue that its tail sported large, arcing, bristly spines until a complete individual with preserved skin was found in the Yixian-Jiufotang. To top things off, the Yixian-Jiufotang has produced the small ornithischian *Tianyulong*, which suggests that insulating fibers were widespread among small dinosaurs. There are new museums in China brimming with enormous numbers of undescribed dinosaur skeletons on display and in storage. Making the Yixian-Jiufotang deposits all the more interesting is that they appear to be the rare remnants of highland lakes thousands of meters above sea level, where chilling winters were similar to those at the poles. Lately coming from central Asia are the cartoonish dromaeosaurs *Halszkaraptor* and *Natovenator*, which may have swum for their prey and grabbed at it with their duck-like heads.

On a global scale, the number of dinosaur trackways that have been discovered is in the many millions. This is logical in that a given dinosaur could potentially contribute only one skeleton to the fossil record but could make innumerable footprints. In a number of locations, trackways are so abundant that they form what have been called "dinosaur freeways." Many of the trackways were formed in a manner that suggests their makers were moving in herds, flocks, packs, and pods. A few may record the attacks of predatory theropods on herbivorous dinosaurs.

The history of dinosaur research is not just one of new ideas and new locations; it is also one of new techniques and technologies. The turn of the twenty-first century has seen paleontology go high tech with the use of computers for processing data and high-resolution CT scanners to peer inside fossils without damaging them. Skeletal and life restorations are being generated in 3-D digital format—whether this has improved the process is another matter. Dinosaurology has also gone microscopic and molecular in order to assess the lives of dinosaurs at a more intimate level, telling us how fast they grew, how long they lived, and at what age they started to reproduce. Bone isotopes are being used to help determine dinosaur diets and to state that

some dinosaurs were semiaquatic. And it turns out that feather pigments can be preserved well enough to restore original colors. Meanwhile the *Jurassic World* franchise helps sustain popular interest in the group even as it presents an obsolete, prefeather image of the birds' closest relations.

The evolution of human understanding of dinosaurs has undergone a series of dramatic transformations since they were scientifically discovered almost two hundred years ago. This is true because dinosaurs are a group of "exotic" animals whose biology was not obvious from the start, unlike fossil mammals or lizards. It has taken time to build up the knowledge base needed to resolve their true form and nature. The latest revolution is still young. When I was a youth, I learned that dinosaurs were, in general, sluggish, cold-blooded, tail-dragging, slow-growing, dim-witted reptiles that did not care for their young. The idea that some were feathered and that birds are living descendants was beyond imagining. Dinosaurology has matured in that it is unlikely that a reorganization of similar scale will occur in the future, but we now know enough about the inhabitants of the Mesozoic to have the basics well established. Sauropods will not return to a hippo-like lifestyle, and dinosaurs' tails will not be chronically plowing through Mesozoic muds. Dinosaurs are no longer so mysterious. Even so, the research is nowhere near its end. To date, over 800 valid dinosaur species in about 500 genera have been discovered and named. This probably represents at most a quarter, and perhaps a much smaller fraction, of the species that have been preserved in sediments that can be accessed. And, as astonishingly strange as many of the dinosaurs uncovered so far have been, there are equally odd species waiting to be unearthed. Reams of work based on as-yet-undeveloped technologies and techniques will be required to provide further details about both dinosaur biology and the world in which they lived. And although a radical new view is improbable, there will be many surprises.



The fuzzy dinosaur *Heterodontosaurus*

WHAT IS A DINOSAUR?

To understand what a dinosaur is, we must first start higher in the scheme of animal classification. The Tetrapoda are the vertebrates adapted for life on land—amphibians, reptiles, mammals, birds, and the like. Amniota comprises those tetrapod groups that reproduce by laying hard-shelled eggs, with the proviso that some have switched to live birth. Among amniotes are two great groups. One is the Synapsida, which includes the archaic pelycosaurs, the more advanced therapsids, and mammals, which are the only surviving synapsids. The other is the Sauropsida, much the same as the Reptilia, all but some early forms of which belong to the great Diapsida, which included most of the ancient marine reptiles that are detailed in the Princeton field guide on that set of creatures. Surviving diapsids include turtles, the lizard-like tuataras, true lizards and snakes, crocodilians, and birds. The Archosauria is the largest and most successful group of diapsids and includes crocodilians and dinosaurs. Birds are literally flying dinosaurs.

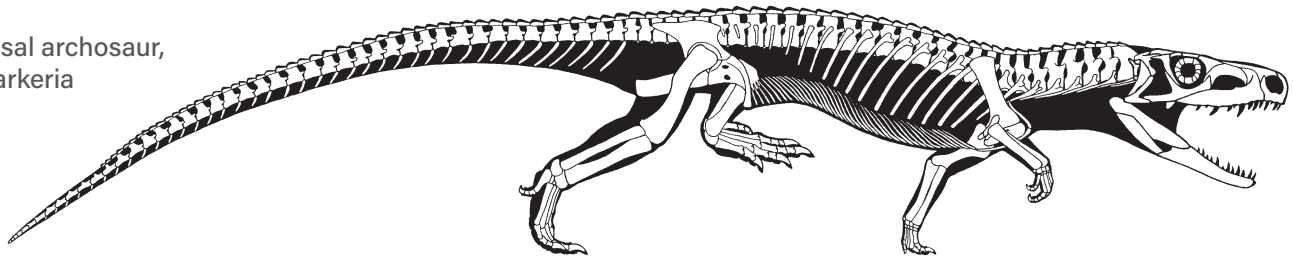
Archosaurs also include the basal forms informally known as thecodonts because of their socketed teeth, themselves a diverse group of terrestrial and aquatic forms that include the ancestors of crocodilians and the winged pterosaurs (covered in another Princeton field guide), although those fliers were not intimate relatives of dinosaurs and birds.

The great majority of researchers now agree that the dinosaurs were monophyletic in that they shared a common ancestor that made them distinct from all other archosaurs, much as all mammals share a single common ancestor that renders them distinct from all other synapsids. This consensus is fairly recent—before the 1970s it was widely thought that dinosaurs came in two distinct types that had evolved separately from thecodont stock, the Saurischia and Ornithischia. It was also thought that birds had evolved as yet another group independently from thecodonts. Dinosauria is formally defined as the phylogenetic clade that includes the common ancestor of *Triceratops* and birds and all their descendants. Because different attempts to determine the exact relationships of the earliest dinosaurs produce somewhat different results, there is some disagreement about whether the most archaic, four-toed theropods were dinosaurs or lay just outside the group. This book includes them, as do most researchers.

In anatomical terms, one of the features that most distinguish dinosaurs centers on the hip socket. The head of the femur is a cylinder turned in at a right angle to the shaft of the femur that fits into a cylindrical, internally open hip socket. This allows the legs to operate in the nearly vertical plane characteristic of the group, with the feet directly beneath the body. You can see this system the next time you have chicken thighs. The ankle is a simple fore-and-aft hinge joint that also favors a vertical leg posture. Dinosaurs were "hind-limb dominant" in that they were either bipedal or, even when they were quadrupedal, most of the animal's weight was borne on the legs, which were always built more strongly than the arms. The hands and feet were generally digitigrade, with the wrist and ankle held clear of the ground. All dinosaurs shared a trait also widespread among archosaurs in general, the presence of large and often remarkably complex sinuses and nasal passages.

Aside from the above basic features, dinosaurs, even when we exclude birds, were an extremely diverse group of animals, rivaling mammals in this regard. Dinosaurs ranged in form from nearly birdlike types such as the sickle-clawed dromaeosaurs to rhino-like horned ceratopsians to armor-plated stegosaurs to elephant- and giraffe-like sauropods and dome-headed pachycephalosaurs. They even took to the skies in the form of birds. However, dinosaurs were limited in that they were persistently terrestrial. Although some dinosaurs may have spent some time feeding in the water like moose or fishing cats, at most a few became strongly amphibious in the manner of hippos, much less marine like seals and whales. The only strongly aquatic dinosaurs are some birds. The occasional statement that there were marine dinosaurs is therefore very incorrect—these creatures of Mesozoic seas were various forms of reptiles that had evolved over the eons.

The situation within dinosaurs is interesting because it has become chaotic. For over a century, dinosaurs have generally been segregated into the two classic groups: the Saurischia, which includes the largely herbivorous sauropodomorphs and the usually predaceous theropods, birds included; and the vegetarian Ornithischia, which despite the name has nothing to do with birds. But while ornithischians are clearly a real, monophyletic clade, the saurischian group has always been weak. Part of the problem is that the earliest species of a given group are all pretty similar to one another, and it is difficult to parse out the few, still subtly different characters that show they are at the base of one of the greater, more sophisticated groups but not the other.

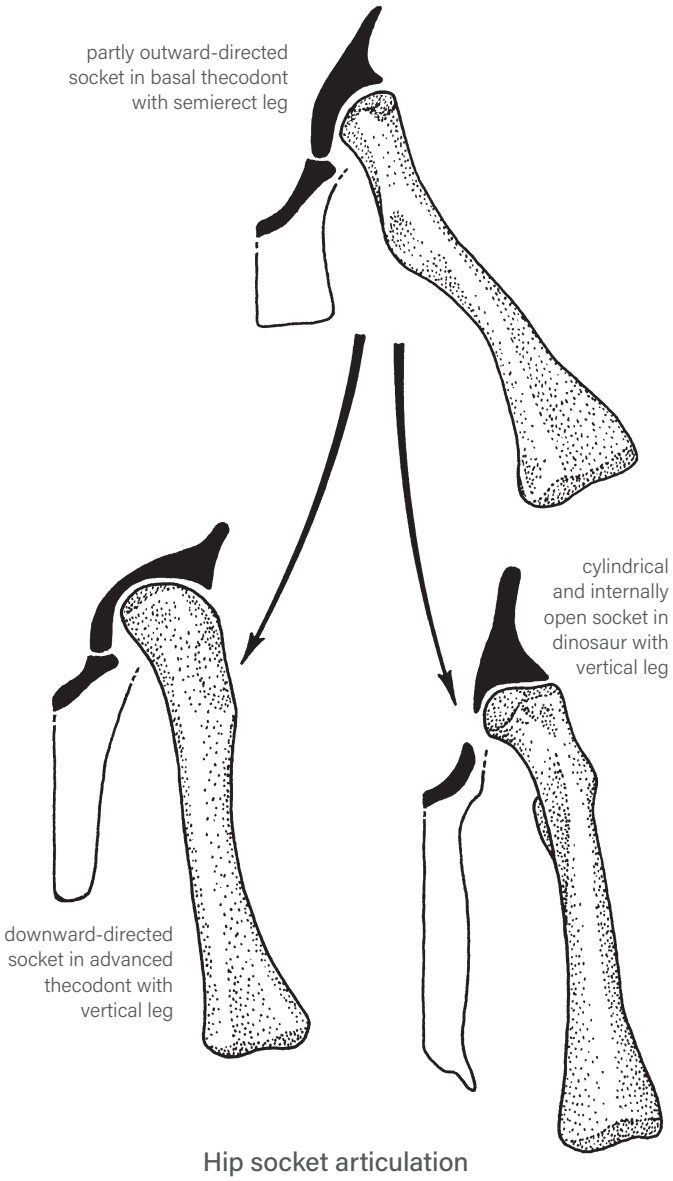


A basal archosaur, Euparkeria

Add to that the incompleteness of the fossil record, and we are missing most of the information needed to sort the situation out. As a result, some researchers have removed the theropods from the Saurischia and more closely allied them with sauropodomorphs in the Ornithoscelida, in which case those dinosaurs not in the latter can be placed in a Paxdinosauria. But there are problems with that scheme too, and it is possible that the herbivorous sauropodomorphs and ornithischians form a joint clade, the Ornithischiformes. All possibilities remain similarly viable at this time; the situation may not be resolvable with the data on hand, if ever, and this volume does not take a firm stand on the issue.

Because birds are dinosaurs in the same way that bats are mammals, the dinosaurs aside from birds are sometimes referred to as "nonavian dinosaurs." This usage can become awkward, and in general in this book dinosaurs that are not birds are, with some exceptions, referred to simply as dinosaurs.

Dinosaurs seem strange, but that is just because we are mammals biased toward assuming the modern fauna is familiar and normal, and past forms are exotic and alien. Consider that elephants are bizarre creatures with their combination of big brains, massive limbs, oversized ears, a pair of teeth turned into tusks, and noses elongated into hose-like trunks. Nor were dinosaurs part of an evolutionary progression that was necessary to set the stage for mammals culminating in humans. What dinosaurs do show is a parallel world, one in which mammals were permanently subsidiary and the dinosaurs show what largely diurnal land animals that evolved straight from similarly day-loving ancestors should actually look like. Modern mammals are much more peculiar, having evolved from nocturnal beasts that came into their own only after the entire elimination of nonavian dinosaurs. While dinosaurs dominated the land, small nocturnal mammals were abundant and diverse, as they are in our modern world. If not for the accidental events that brought the Age of Dinosaurs to a quick end, dinosaurs would probably still be the global norm.



Hip socket articulation in archosaurs

DATING DINOSAURS

How can we know that dinosaurs lived in the Mesozoic, first appearing in the Late Triassic over 230 million years ago and then disappearing at the end of the Cretaceous 66 million years ago?

As gravels, sands, and silts are deposited by water and sometimes wind, they build up in sequence atop the previous layer, so the higher in a column of deposits a dinosaur is, the younger it is relative to dinosaurs lower in the sediments. Over time, sediments form distinct stratigraphic beds that are called formations. For example, *Apatosaurus*, *Brontosaurus*, *Diplodocus*, *Barosaurus*, *Stegosaurus*, *Camptosaurus*, *Allosaurus*, and *Ornitholestes* are found in the Morrison Formation of western North America, which was laid down in the Late Jurassic, from 150 to 156 million years ago. Deposited largely by rivers over an area covering many states in the continental interior, the Morrison Formation is easily distinguished from the marine Sundance Formation lying immediately below as well as from the similarly terrestrial Cedar Mountain Formation above, which contains very different sets of dinosaurs. Formed over millions of years, the Morrison is subdivided into lower (older), middle, and upper (younger) levels. So a fossil found in the Sundance is older than one found in the Morrison, a dinosaur found in the lower Morrison is older than one found in the middle, and a dinosaur from the Cedar Mountain is younger still.

Geological time is divided into a hierarchical set of names. The Mesozoic is an era—preceded by the Paleozoic

and followed by the Cenozoic—that contained the three progressively younger periods called the Triassic, Jurassic, and Cretaceous. These are then divided into Early, Middle, and Late, except that the Cretaceous is split only into Early and Late despite being considerably longer than the other two periods (this was not known when the division was made in the 1800s). The periods are further subdivided into stages. The Morrison Formation, for example, began to be deposited during the last part of the Oxfordian and continued through the entire Kimmeridgian. Lasting 40 million years, the Cedar Mountain Formation spans all or part of seven stages of nearly all the Early Cretaceous into the beginning of the Late Cretaceous.

The absolute age of recent fossils can be determined directly by radiocarbon dating. Dependent on the ratios of carbon isotopes, this method works only on bones and other organic fossils going back up to 50,000 years, far short of the dinosaur era. Because it is not possible to directly date Mesozoic dinosaur remains, we must instead date the formations that the specific species are found in. This is viable because a given dinosaur species lasted only a few hundred thousand to a few million years.

The primary means of absolutely determining the age of dinosaur-bearing formations is radiometric dating. Developed by nuclear scientists, this method exploits the fact that radioactive elements decay in a very precise manner over time. The main nuclear transformations used are uranium to lead, potassium to argon, and one argon isotope to another argon isotope. This system requires the presence of volcanic deposits that initially set the nuclear clock. These deposits are usually in the form of ashfalls, similar to the one deposited by Mount Saint Helens over neighboring states, that leave a distinct layer in the sediments. Assume that one ashfall was deposited 144 million years ago, and another one higher in the sediments 141 million years ago. If a dinosaur is found in the deposits in between, then we know that the dinosaur lived between 144 and 141 million years ago. As the technology advances and the geological record is increasingly better known, radiometric dating is becoming increasingly precise. The further back in time one goes, the greater the margin of error, and the less exactly the sediments can be dated. In many cases the dating is well set and not likely to change—the end of the Mesozoic happened just a dash over 66 million years ago. In other cases, less favorable geological circumstances leave matters less precisely settled; when the second edition of this book was prepared, the shift from the Oxfordian to the Kimmeridgian stage was calculated to have occurred less than 155 million years ago, but it was just updated to over 157 million, a value that may change based on further research.

Because it was not possible to accurately date geological deposits when the time divisions were mapped and named in the 1700s and 1800s, they later proved to be very irregular in the amount of time covered by each division; for instance, the Norian stage is about 10 times longer than the Hettangian stage.

Volcanic deposits are often not available, and other methods of dating must be used. Doing so requires biostratigraphic correlation, which can in turn depend in part on the presence of "index fossils." Index fossils are organisms, usually marine invertebrates, that are known to have existed for only geologically brief periods of time, just a few million years at most. Assume a dinosaur species is from a formation that lacks datable volcanic deposits. Also assume that the formation grades into marine deposits laid down at the same time near its edge. The marine sediments contain organisms that lasted for only a few million years or less. Somewhere else in the world, the same species of marine life was deposited in a marine formation that includes volcanic ashfalls that have been radiometrically dated to between 83 and 81 million years. We can then conclude that the dinosaur in the first formation is also 83 to 81 million years old.

A number of dinosaur-bearing formations lack both volcanic deposits and marine index fossils. It is often not possible to accurately date the dinosaurs in these deposits. It is only possible to broadly correlate the level of development of the dinosaurs and other organisms in the formation with faunas and floras in better-dated formations, and this produces only approximate results. This situation is especially common in central Asia. The reliability of dating therefore varies. It can be very close to the actual value in formations that have been well studied and contain volcanic deposits; these can be placed in specific parts of a stage. At the other extreme are those formations that, because they lack the needed age determinants, and/or because they have not been sufficiently well examined, can only be said to date from the early, middle, or late portion of one of the periods, an error that can span well over 10 million years. North America currently has the most robust linkage of the geological time scale with its fossil dinosaurs on Earth.

THE EVOLUTION OF DINOSAURS AND THEIR WORLD

Dinosaurs appeared in a world that was both ancient and surprisingly recent—it is a matter of perspective. The human view that the time of Mesozoic dinosaurs was remote in time is an illusion that results from our short life span. A galactic year, the time it takes our solar system to orbit the center of the galaxy, is 200 million years. Only one galactic year ago the dinosaurs had just appeared on planet Earth. When dinosaurs first emerged, our solar system was already well over four billion years old, and 95 percent of the history of our planet had already passed. A time traveler arriving on Earth when dinosaurs first existed would have found it both comfortingly familiar and marvelously different from our time.

As the moon slowly spirals out from the Earth because of tidal drag, the length of each day grows. When dinosaurs initially evolved, a day was about 22 hours and 45 minutes long, and the year had around 385 days; when they went largely extinct, a day was up to 23 hours and over 30 minutes, and the year was down to 371 days. The moon would have looked a little larger and would have more strongly masked the sun during eclipses—there would have been none of the rare annular eclipses in which the moon is far enough away in its elliptical orbit that the sun rings the moon at maximum. The "man on the moon" leered down upon the dinosaur planet, but the prominent Tycho crater was not blasted into existence until toward the end of the Early Cretaceous. As the sun converts an increasing portion of its core from hydrogen into denser helium, it becomes hotter by nearly 10 percent every billion years, so the sun was about 2 percent cooler when dinosaurs first showed up and around a half percent cooler than it is now when most went extinct.

At the beginning of the great Paleozoic era over half a billion years ago, the Cambrian Revolution saw the advent of complex, often hard-shelled organisms. Also appearing were the first simple vertebrates. As the Paleozoic progressed, first plants and then animals, including tetrapod vertebrates, began to invade the land, which saw a brief Age of Amphibians in the late Mississippian followed by the classic Age of Reptiles in the Pennsylvanian and much of the Permian. By the last period in the Paleozoic, the Permian, the continents had joined together into the C-shaped supercontinent Pangaea, which straddled the equator and stretched nearly to the poles north and south. Lying like a marine wedge between the terrestrial arms of northern Laurasia and southern Gondwanaland was the great Tethys tropical ocean; all that is left of that is the modest Mediterranean. Seventy percent of the world was dominated by the enormous Panthalassic superocean, whose vast expanse was marred only by occasional islands; the Pacific is its somewhat lesser descendant. With the majority of land far from the oceans, most terrestrial habitats were harshly semiarid, ranging from extra hot in the tropics to sometimes glacial at high latitudes. The major vertebrate groups had evolved by that time. Among synapsids, the mammal-like therapsids, some up to the size of rhinos, were the dominant large land animals in the Age of Therapsids of the Late Permian. These were apparently more energetic than reptiles, and those living in cold climates may have used fur to conserve heat. Toward the end of the period, the first archosaurs appeared. These low-slung, vaguely lizard- or crocodilian-looking creatures were a minor part of the global fauna. The conclusion of the Permian was marked by a great extinction that is attributed to the massive volcanism then forming the enormous Siberian Traps—there is no evidence of a major meteorite impact at the time—which so heavily contaminated the atmosphere in multiple ways that the global environment was severely disrupted chemically and weatherwise. In some regards the P/T extinction exceeded that which killed off the terrestrial dinosaurs 185 million years later.

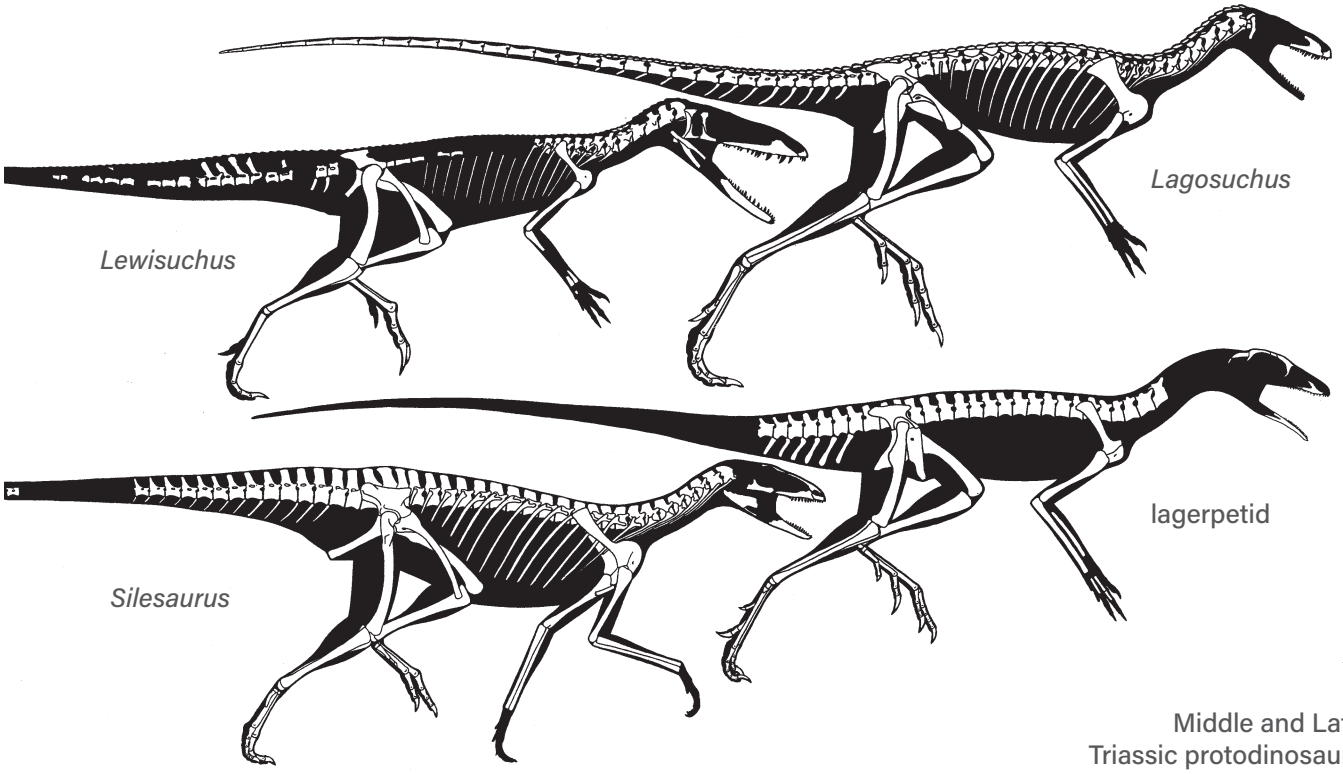
At the beginning of the first period of the Mesozoic, the Triassic, the global fauna was severely denuded. As it recovered, the few remaining therapsids enjoyed a second evolutionary radiation and again became an important part of the wildlife. And again, they never became truly enormous or tall, although a few late examples were as big as small elephants. This time they had serious competition, as the archosaurs also underwent an evolutionary explosion, first expressed as a wide variety of thecodonts, some of which reached a tonne in mass. One group evolved into aquatic, armored crocodile mimics. Others became armored land herbivores. Most were terrestrial predators that moved on erect legs achieved in a manner different from dinosaurs. The head of the femur did not turn inward; instead, the hip socket expanded over the femoral head until the shaft could be directed downward. Some of these erect-legged archosaurs were nearly bipedal. Others became toothless plant eaters. It is being realized that in many respects the Triassic thecodonts filled the lifestyle roles that would later be occupied by dinosaurs. Even so, these basal archosaurs never became gigantic or very tall. Also coming onto the scene were the crocodilians, the only group surviving today that reminds us what the archosaurs of the Triassic were like. Triassic crocodilians started out as small, long-legged, digitigrade land runners. Their sophisticated liver-pump lung systems probably evolved to help power a highly aerobic exercise ability. Crocodilians, like many of the thecodonts, had a very undinosaurian feature. Their ankles were complex, door-hinge-like joints in which a tuber projecting from one of the ankle bones helped increase the leverage of the muscles on the foot, rather as in mammals. In the Norian, a modest extinction event cut back somewhat on the diversity of therapsids and thecodonts. In the Late Triassic, the membrane-winged, long-tailed pterosaurs show up in the fossil record fully formed, since their evolution had started earlier. Pterosaurs having the same kind of simple-hinge ankle seen in dinosaurs is evidence that the two groups are related, forming the Ornithodira. The energetic pterosaurs were insulated; we do not yet know whether other nondinosaurian archosaurs were also covered with thermal fibers, but the possibility is substantial.

By the middle Triassic, quite small predatory archosaurs were evolving that exhibited a number of features of dinosaurs. Although the hip socket was still not internally open, the femoral head was turned inward, allowing the legs to operate in a predominantly vertical plane. The ankle was the simple fore-aft hinge that remains in birds. The skull was lightly constructed. At first recorded as skeletal remains in the early Late Triassic of South America—trackways suggest they appeared earlier in the period—protodinosaurs have since been found on other continents. These bipedal/quadrupedal early near dinosaurs would survive only until the Norian as they were

displaced by their descendants. Protodinosaurs show that dinosaurs started out as little creatures; big dinosaurs did not descend from the big basal archosaurs.

From small things big things can evolve, and very quickly. In the Carnian stage of the Late Triassic the fairly large-bodied, small-hipped, four-toed herrerasaur predators were on the global stage. These fully bipedal early dinosaurs with cylindrical hip joints dwelled in a world still dominated by complex-ankled archosaurs and would not last beyond the Norian or maybe the Rhaetian stage, perhaps because these early dinosaurs did not have an aerobic capacity high enough to vie with their newer dinosaurian competitors. The Norian saw the appearance of the great group that is still with us, the bird-footed avepod theropods, whose enlarging hips and beginnings of the avian-type respiratory system imply a further improvement in aerobic performance and thermoregulation. At about the same time, the first members of one of the grand groups of herbivorous dinosaurs are recorded in the fossil record, the small-hipped, semibipedal prosauropods with lightly built heads and slender teeth best suited for tender vegetation such as ferns. Whether prosauropods also had bird-style respiration is a matter of debate; if so, it was weakly developed. All these new dinosaurs gave therapsids and thecodonts increasing competition as they rapidly expanded in diversity as well as size. Just 15 or 20 million years after the evolution of the first little protodinosaurs, prosauropods weighing 2 tonnes had developed. In only another 10 million years, prosauropods as big as elephants were extant, becoming the first truly gigantic land animals. These long-necked dinosaurs were also the first herbivores able to browse at high levels, many meters above the ground. Dinosaurs were showing the ability to evolve large dimensions and bulk on land, an attribute otherwise seen only among a few therapsids, mainly mammals. In the Carnian, the first of the beaked herbivorous ornithischians arrived. These little semibipeds were not common, and they, as well as small theropods and prosauropods, may have dug burrows as refuges from a predator-filled world. By the last stage of the Triassic, avepod and prosauropod dinosaurs were becoming the ascendant land animals, although they still lived among a number of thecodonts and some therapsids. From the latter, at this time, evolved the first mammals. Mammals and dinosaurs have therefore shared the planet for over 200 million years—but for 140 million of those years, mammals remained small.

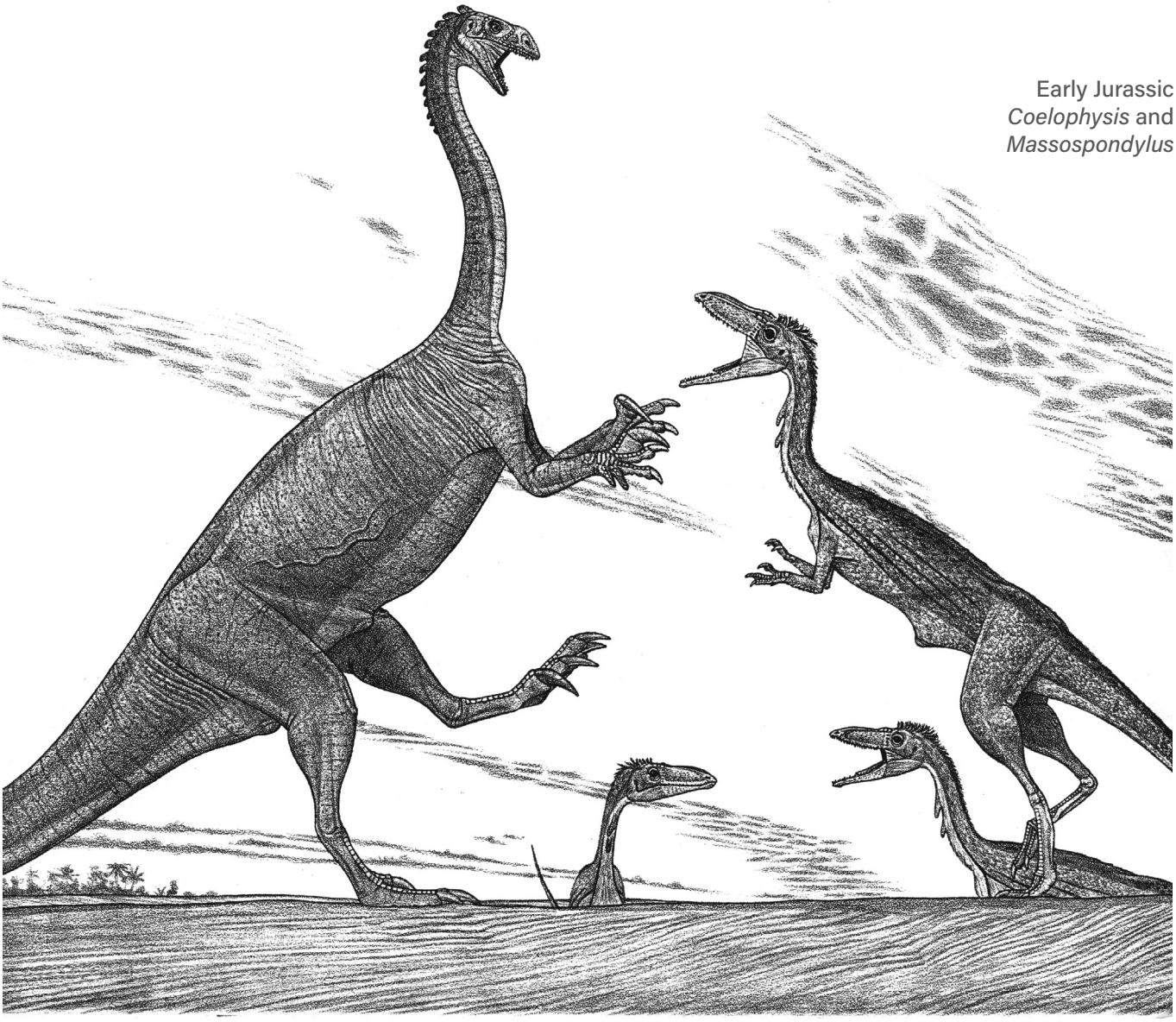
Because animals could wander over the entire supercontinent with little hindrance from big bodies of water, faunas tended to exhibit little difference from one region to another. And with the continents still collected together, the climatic conditions over most of the supercontinent remained harsh. It was the greenhouse world that would prevail through the Mesozoic. The carbon dioxide level was two to ten times higher than it is currently, boosting temperatures to such highs—despite the slightly cooler sun of those times—that even the polar regions were relatively warm in winter. The low level of tectonic activity meant there were few tall mountain ranges to capture rain or interior seaways to provide moisture. Hence, there were great deserts, and most of the vegetated lands were seasonally



Middle and Late Triassic protodinosaurs

semiarid, but forests were located in the few regions of heavy rainfall and groundwater created by climatic zones and rising uplands. It appears that the tropical latitudes were so hot and dry that the larger dinosaurs, with their high energy budgets, could not dwell near the equator and, except for tenuous coastal strips, were restricted to the cooler, wetter, higher latitudes. The flora was in many respects fairly modern and included many plants we would be familiar with. Wet areas along watercourses were the domain of rushes and horsetails. Some ferns also favored wet areas and shaded forest floors. Other ferns grew in open areas that were dry most of the year, flourishing during the brief rainy season. Large parts of the world may have been covered by fern prairies, comparable to the grasslands and shrublands of today. Tree ferns were common in wetter areas. Even more abundant were the fernlike or palmlike cycadeoids, similar to the cycads that still inhabit the tropics. Taller trees included water-loving ginkgoaceans, of which the maidenhair tree is the sole—and, until widely planted in urban areas, the nearly extinct—survivor. Dominant among plants were conifers, most of which at that time had broad leaves rather than needles. Some of the conifers were giants rivaling the colossal trees of today, such as those that formed the famed Petrified Forest of Arizona. Flowering plants were completely absent.

The end of the Triassic about 200 million years ago saw another extinction event. A giant impact had occurred in the hard, ancient rocks of southeastern Canada, but it was a few million years before the specific time of the extinction. Coincident with the extinction were intense volcanics tied to the formation of the budding Atlantic Ocean—note that volcanism was not especially common in the Mesozoic relative to the subsequent Cenozoic. The heavy dusting of the atmosphere with reflective aerosol debris cooled off the planet to the degree that minor glaciations occurred at high latitudes. The thecodonts and



Early Jurassic
Coelophysis and
Massospondylus

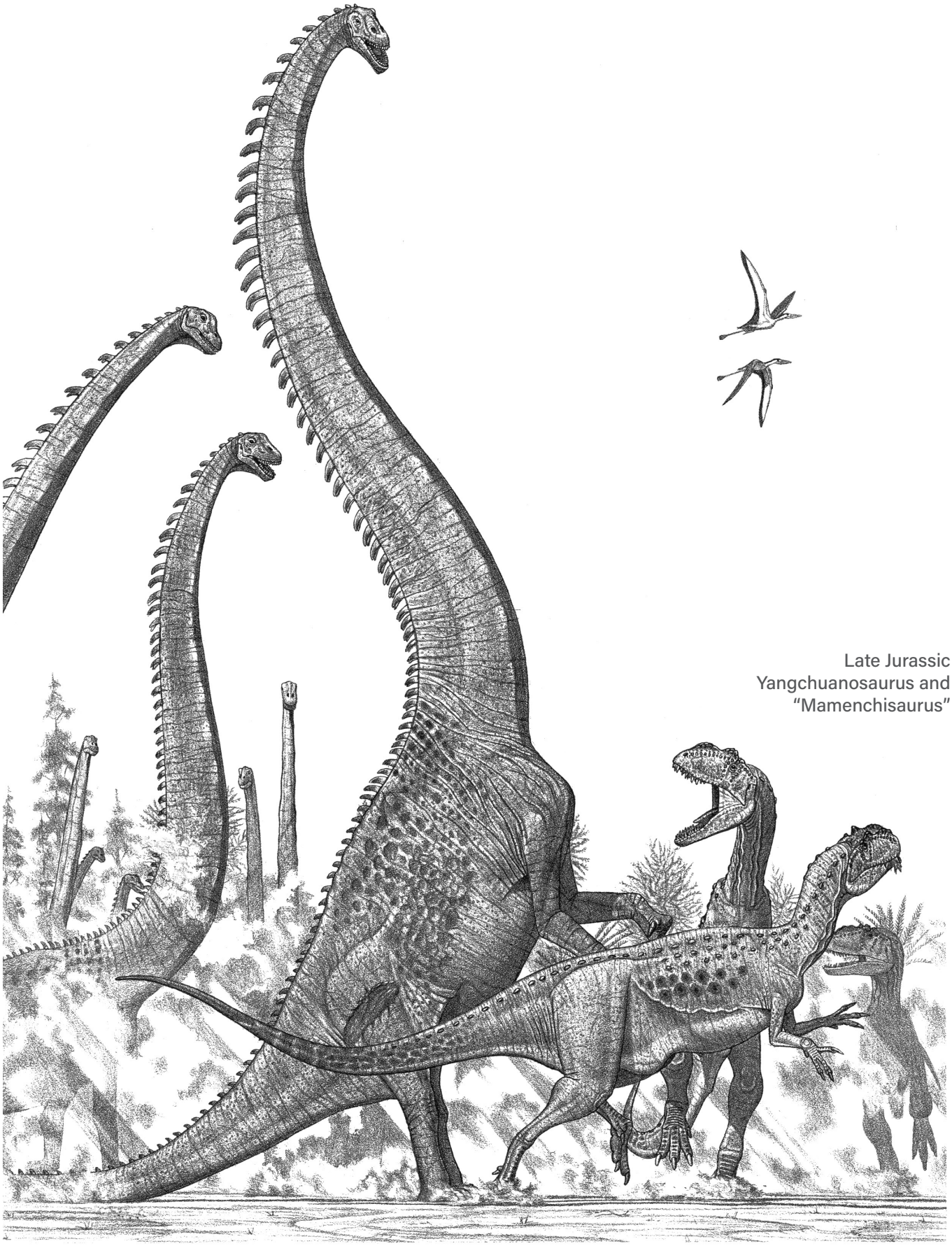
therapsids suffered the most: the former were wiped out with the exception of crocodilians, and only scarce remnants of the latter survived along with furry mammal relatives. The more energetic, sometimes insulated pterosaurs and dinosaurs were able to deal with the big chills without difficulty and sailed through the crisis into the Early Jurassic with little disruption, so much so that avepod theropods such as *Coelophysis* remained common and little changed, as did prosauropods. For the rest of the Mesozoic, dinosaurs would enjoy almost total dominance on land except for some substantial semiterrestrial crocodilians; otherwise there simply were no competitors above a few kilograms in weight. Such extreme superiority was unique in Earth's history. The Jurassic and Cretaceous combined were the Age of Dinosaurs.

The big novelty of the Early Jurassic was the advent of the sauropods that had descended from prosauropods—recent claims that sauropods first appeared in the Late Triassic have not borne out. Some quadrupeds that were elephantine in both size and body and leg form, with very long necks and tails added, got as big as bull African elephants. Never small bodied, their columnar legs meant these were the first dinosaurs not able to achieve a full run, so being big was necessary for defense. As the Jurassic progressed, the prosauropods appear to have been unable to compete with their more sophisticated, big-hipped sauropod relatives and were gone by the end of the Early Jurassic. Also out were the coelophysoid avepods in favor of the bigger-hipped averostrans with more powerful leg muscles that began to show up in the Early Jurassic. It is likely that the loss of Triassic grade dinosaurs in favor of more modern sauropods and averostrans was finalized by another bout of mass volcanism, this time in southern Gondwana in the late Early Jurassic, which is associated with tough conifers becoming the dominant trees during the rest of the Jurassic into the Cretaceous. Sauropods' stouter skulls and teeth atop stronger necks apparently rendered them better able to deal with the harder-to-chew flora. Larger hip muscles and an increasingly well-developed birdlike respiratory system suggest that sauropods had the higher aerobic capacity and higher-pressure circulatory system needed to achieve truly great height and bulk. Although some theropods were getting moderately large, the much more gigantic adult sauropods enjoyed a period of relative immunity from attack. Ornithischians remained uncommon, and one group was the first set of dinosaurs to develop armor protection. Those started out mainly bipedal and then quickly switched to the more quadrupedal gait best suited for supporting their suits of armor. Another group of ornithischians was the small, chisel-toothed, semibipedal heterodontosaurs, which established that fiber coverings had evolved in some small dinosaurs by this time, if not earlier. On the continents, crocodilians remained small and fully or partly terrestrial, while other groups became marine giants.

Farther west, the supercontinent was beginning to break up, creating African-style rift valleys along today's Eastern Seaboard of North America that presaged the opening of the Atlantic. Even so, Europe remained an Indonesia-like archipelago of islands immediately northeast of North America, as it had been for a long while. More importantly for dinosaur faunas, the increased tectonic activity in the continent-bearing conveyor belt formed by the mantle caused the ocean floors to lift up, spilling the oceans onto the continents in the form of shallow seaways that began to isolate different regions from one another, encouraging the evolution of a more diverse global wildlife. The expansion of so much water onto the continents also raised rainfall levels, although most habitats remained seasonally semiarid. The increased rain helped cool the continents some, allowing big dinosaurs to roam about at all latitudes. The moving land masses also produced more mountains able to squeeze rain out of the atmosphere.

Beginning 175 million years ago, the Middle Jurassic began the long Age of Sauropods, whose increasingly sophisticated respiratory and circulatory systems allowed them to match medium-sized whales in bulk and trees in height. Sauropods thrived even in dry habitats by feeding on the open, conifer-dominated forests that spread over flats and lined watercourses, as well as the fern prairies in the wet season. In China, partly isolated by seaways, some mid-Jurassic sauropods evolved slender necks so long that they could feed 10 m (over 30 ft) high, and by the end of the stage the height maximum had topped off at six to seven stories on animals of three dozen tonnes. A few sauropods had tail clubs. Also appearing were the first small, armored stegosaur ornithischians that also introduced tail spikes. Even smaller were the little ornithopods, the beginnings of a group of ornithischians whose respiratory systems—which may have paralleled those of mammals—and dental batteries gave them great evolutionary potential. Although the increasingly sophisticated tetanuran, avetheropod, and coelurosaur theropods evolved and featured highly developed avian-type respiratory systems, for reasons that are obscure, they continued to fail to produce true giants, those yet known reaching barely a tonne at most. There is tenuous evidence that flowering plants were present by the middle of the Jurassic, but if so they were not yet common.

The Late Jurassic, which began 160 million years ago, was the apogee of two herbivorous dinosaur groups, the sauropods and the stegosaurs. Sauropods, which included mamenchisaurs, haplocanthosaurs, dicraeosaurs, diplodocines, apatosaurines, camarasaurs, and brachiosaurs, would never again be so diverse. Some neosauropods rapidly enlarged to 50 to 75 tonnes, and a few may have greatly exceeded 100 tonnes, rivaling the biggest baleen whales. But it was a time of growing danger for the sauropods: theropods had finally evolved hippo-sized megalosaurs, yangchuanosaurs, and allosaurs that could tackle the colossal herbivores. Meanwhile, some sauropods isolated on islands underwent dwarfing to rhino size to better accommodate to the limited resources (the same would happen to elephants and hippos). The now rhino- and



Late Jurassic
Yangchuanosaurus and
"Mamenchisaurus"

sometimes elephant-sized stegosaurs were at their most diverse. Some developed spectacular plate arrays, while others mimicked sauropods a little and had fairly long necks. Having evolved columnar legs, these dinosaurs also could not run. But the other group of big armored dinosaurs, the short-legged ankylosaurs sans tail clubs, was beginning to develop. Also entering the fauna were the first fairly large ornithopods, sporting thumb spikes. Asia saw the development of small semibipedal ceratopsians.

The still long-armed ancestors of tyrannosaurs seem to have been developing at this time, and assorted gracile coelurosaurs were numerous. But it is the advent of the highly birdlike and partly arboreal airfoilans at the end of the mid-Jurassic going into the late part of the period that was a major event, and these survived until today. Initial dinosaur flight appears to have come in two versions. One experiment was the bat-winged scansoriopterygids of Asia; these apparently soon disappeared, perhaps because of competition from the bird-winged aveairfoilans. More important for the long-term future of dinosaurs of the air were Chinese deinonychosaur anchiornids, the earliest dinosaurs known to have had large feathers on their arms as well as legs. Because the moderately long, symmetrical feathers were not proper airfoils despite the great length of the arms, these apparent climbers may—or may not—be the first example of a reduction of flight abilities from an ancestor with superior aerial prowess. A few million years later, when Europe was still a nearshore extension of northeastern North America, the first "bird," the deinonychosaur *Archaeopteryx*, was extant. Preserved in lagoonal deposits on the northwestern edge of the then great Tethys Ocean, it had a combination of very large arms and long, asymmetrical wing feathers indicating that it was developing the early stages of powered flight. Also found in the deposits is fragmentary *Alcmonavis*, the first avian to have an expanded central finger base to better support the outer flight feathers. The advent of the little aveairfoilans also heralded the first major increase in dinosaurian mental powers, as brain size and complexity rose to the lower avian level. Pterosaurs, which retained smaller brains, remained small bodied, and most still had long tails. Although some crocodilians were still small runners, the highly amphibious crocodilians of the sort we are familiar with were appearing, though they were not particularly large. That there were no big freshwater armored archosaurs in the Jurassic is another paleomystery. Their liver-pump lung systems readapted into buoyancy control devices. Although small, mammals were undergoing extensive evolution in the Jurassic. Many were insectivorous or herbivorous climbers, but some were burrowers, and others had become freshwater-loving swimmers. Dinosaurs did not yet show signs of being specifically adapted for life in the water, for reasons that remain obscure.

During the Middle and Late Jurassic, carbon dioxide levels were incredibly high, with the gas making up between 5 percent and 10 percent of the atmosphere, 10 to 20 times twenty-first-century levels (and about twice preindustrial norms). As the Jurassic and the classic Age of Sauropods ended, the incipient North Atlantic was about as large as today's Mediterranean. Vegetation had not yet changed dramatically from the Triassic. Wetter areas were dominated by conifers similar to cypress. A widespread and diverse conifer group of the time was the araucarians. Some appear to have evolved a classic umbrella shape in which most of the adult trunk was as bare of foliage as a telephone pole, with all the branches concentrated at the top. Still seen in a few South American examples, this odd shape may have evolved as a means of escaping browsing by the ever-hungry sauropods, which should have had a profound impact on floral landscapes as they heavily browsed and wrecked trees to an extent that probably exceeded that of elephants. What happened to the fauna at the end of the Jurassic is not well understood because of a lack of deposits. Some researchers think there was a major extinction, in part because new data are showing that the very different Early Cretaceous dinofaunas were up and running closer to the J/K boundary than was thought, maybe even a little before, indicating a sudden and fast turnover of the type that is usually evidence of a major global disruption. For example, why did the sophisticated diplodocids, with their exceptional feeding flexibility, go extinct, especially when the titanosaurs would later evolve horselike heads with pencil teeth, and whip tails? There is not yet obvious geological evidence of a big bad event at the time.

Whatever did or did not happen, the great Cretaceous began some 145 million years ago. This 80-million-year-long period would see an explosion of dinosaur evolution that surpassed all that had gone before as the continents continued to split, the south Atlantic began to open, India detached from Antarctica and then Madagascar as it began to head toward Asia, and seaways crisscrossed the continents. Greenhouse conditions became less extreme as carbon dioxide levels gradually edged downward, with a quick sharp drop near the end of the Valanginian that looks like it led to polar glaciers on a limited scale. Not that carbon dioxide levels dropped to the modern preindustrial level. Early in the Cretaceous, the warm Arctic oceans generally kept conditions up there balmy even in winter. At the other pole, continental conditions rendered winters frigid enough to form permafrost. General global conditions were a little wetter than they were earlier in the Mesozoic, but seasonal aridity remained the rule in most places, and true rain forests continued to be scarce at best.

Sauropods remained abundant and often enormous, but they were less diverse than before, as a few small-bodied, short-necked diplodocoids—some with broad, square-ended mouths specialized for grazing—tall brachiosaurs, and especially the broad-bellied titanosaurs predominated. Yet their time of overwhelming dominance was past.

To a fair extent the Cretaceous was the Age of Ornithischians. Ornithopods small and especially large flourished. Thumb-spiked iguanodonts soon became common herbivores in the Northern Hemisphere. Their well-developed

plant-pulping dental batteries may have been a key to their success. A few evolved tall sails formed by their vertebral spines. Among ceratopsians, the small Asian chisel-toothed psittacosaurs first proliferated, and their relatives, the big-headed protoceratopsids, appeared in the same region. So did the first of the dome-headed pachycephalosaurs. Stegosaurs, however, soon departed the planet, the second and final major herbivorous dinosaur group to become extinct since the prosauropods. This reveals that over time, the dinosaurs tended to add new groups without losing many of the old ones, building up their diversity over the Mesozoic. In the place of stegosaurs, the low-slung and extremely fat-bellied armored ankylosaurs became a major portion of the global fauna, their plates and spikes providing protection from the big Laurasian allosauroids, some of which had back sails, and the snub-nosed, short-armed abelisaurs in Gondwana. Another group of giant theropods, the croc-snouted spinosaurs, apparently adapted to catch fish as part of their diet. Bone isotopes indicate that spinosaurs were semiaquatic like hippos, making them the first dinosaur group to become fairly water loving.

It was among the smaller theropods that dinosaur evolution really went wild in the Early Cretaceous. Coming along evolution-wise were the Northern Hemisphere tyrannosauroids, sometimes large and heavily feathered, and still large armed. And the first of the ostrich-mimicking ornithomimosaurs were present. But the focus of events was among the nearly avian aveairfoilans. As revealed by the spectacular volcanic highland lake deposits of northeastern China, deinonychosaurs developed into an array of flying and flightless forms, with the latter probably secondarily flightless descendants of the fliers. The famous sickle-clawed dromaeosaurs appear to have begun as small aerialists with two sets of wings, the normal ones on the arms and an equally large set on the hind legs. From these appear to have evolved bigger terrestrial dromaeosaurs that hunted larger game. The other major sickle-clawed Cretaceous deinonychosaur group, the more lightly built and swifter-running troodonts, also thrived.

At the same time, not only had birds themselves descended from deinonychosaur dinosaurs, but the Chinese deposits show they had already undergone a spectacular evolutionary radiation by 125 million years ago. Some retained teeth; others were toothless. Some had long tails; most did not. None were especially large. Among these early birds were the toothed, long-skulled, and long-tailed herbivorous jeholornithiformes. It is possible that they were the ancestral type for the enigmatic, potbellied, landbound therizinosaur dinosaurs that sported tellingly similar skulls. And the deep, parrot-beaked omnivoropterygid birds in turn bear a striking resemblance to the similarly deep-headed and short-tailed protarchaeopterygid and caudipterid oviraptorosaurs from the same formations. There is good reason to propose that the short-tailed oviraptorosaurs were yet another group of secondarily flightless dinosaur-birds, ones more advanced than the long-tailed

The flying dinosaur *Sinornithosaurus* attacking *Psittacosaurus*

archaeopterygian-dromaeosaur-troodont deinonychosaurs and the therizinosaurs. The conventional view held by most researchers is that flightless therizinosaurs and oviraptorosaurs happened to be merely convergent with the flying jeholornithiformes and omnivoropterygids, respectively.

Pterosaurs, now short tailed and consequently more dynamic fliers, were becoming large as they met increasing competition from birds. Also fast increasing in size were the freshwater crocodilians, making them an increasing threat for dinosaurs coming to water to drink or for other purposes. Some large crocodilians were semiterrestrial and able to attack big dinosaurs on land as well as in the water. Still scampering about were a few small running crocodilians. Some carnivorous mammals were big enough, about a dozen kilograms, to catch and consume the smallest dinosaurs and their babies. Even gliding mammals had evolved by this time.

During the late Early Cretaceous a major evolutionary event occurred, one that probably encouraged the rapid evolution of dinosaurs. Flowering plants began to become an important portion of the global flora. The first examples were small shrubs growing along shifting watercourses where their ability to rapidly colonize new territory was an advantage. Others were more fully aquatic, including water lilies. Their flowers were small and simple. The fast growth and strong recovery potential of flowering plants may have encouraged the development of low-browsing ankylosaurs

and ornithopods. Conversely, the browsing pressure of dinosaurs may have been a driving force behind the evolution of the fast-spreading and fast-growing new plants.

In the Late Cretaceous, which began 100 million years ago, with the continental breakup well under way, the Panthalassic colossus became the great Pacific, and interior seaways often covered vast tracts of land. As carbon dioxide levels continued to drop, the dark Arctic winters became cold enough to match the conditions seen in today's high northern forests, and glaciers crept down high-latitude mountains. Early in the Late Cretaceous the moisture-loving dawn redwood, a now rare and atypically deciduous conifer, evolved to cope with the dark circumpolar winters. Mammals were increasingly modern—and still small. Pterosaurs, marine and terrestrial, became gigantic to a degree that stretches credulity. Oceanic pteranodonts had wings stretching 8 m (over 25 ft). Toward the end of the Cretaceous, the freshwater-loving azhdarchids sported wings of 11 m (over 35 ft) and easily outweighed ostriches. Whether the diversity of membrane-winged pterosaurs went into decline in the Late Cretaceous—with little or nothing in the way of small adults because of their inability to directly compete with feather-winged birds, or because the flying juveniles of the giants displaced small pterosaurs, or both—is a matter of discussion. Small, running crocodilians remained extant, and a few even became herbivorous. As for the conventional freshwater crocodilians, in some locales they become colossi up to 12 m (close to 40 ft) long and approaching 10 tonnes, as large as the biggest flesh-eating theropods. Although these monsters fed mainly on fish and smaller tetrapods, they posed a real threat to all but the largest dinosaurs coming to the water to drink or swimming across large bodies of water. The hazard should not be exaggerated, however, because these supercrocs do not appear to have been very numerous in many locations, were absent at higher latitudes, and did not last all that long. Even so, their existence may have discouraged the evolution of profoundly aquatic dinosaurs, none of which went fully aquatic, much less marine.

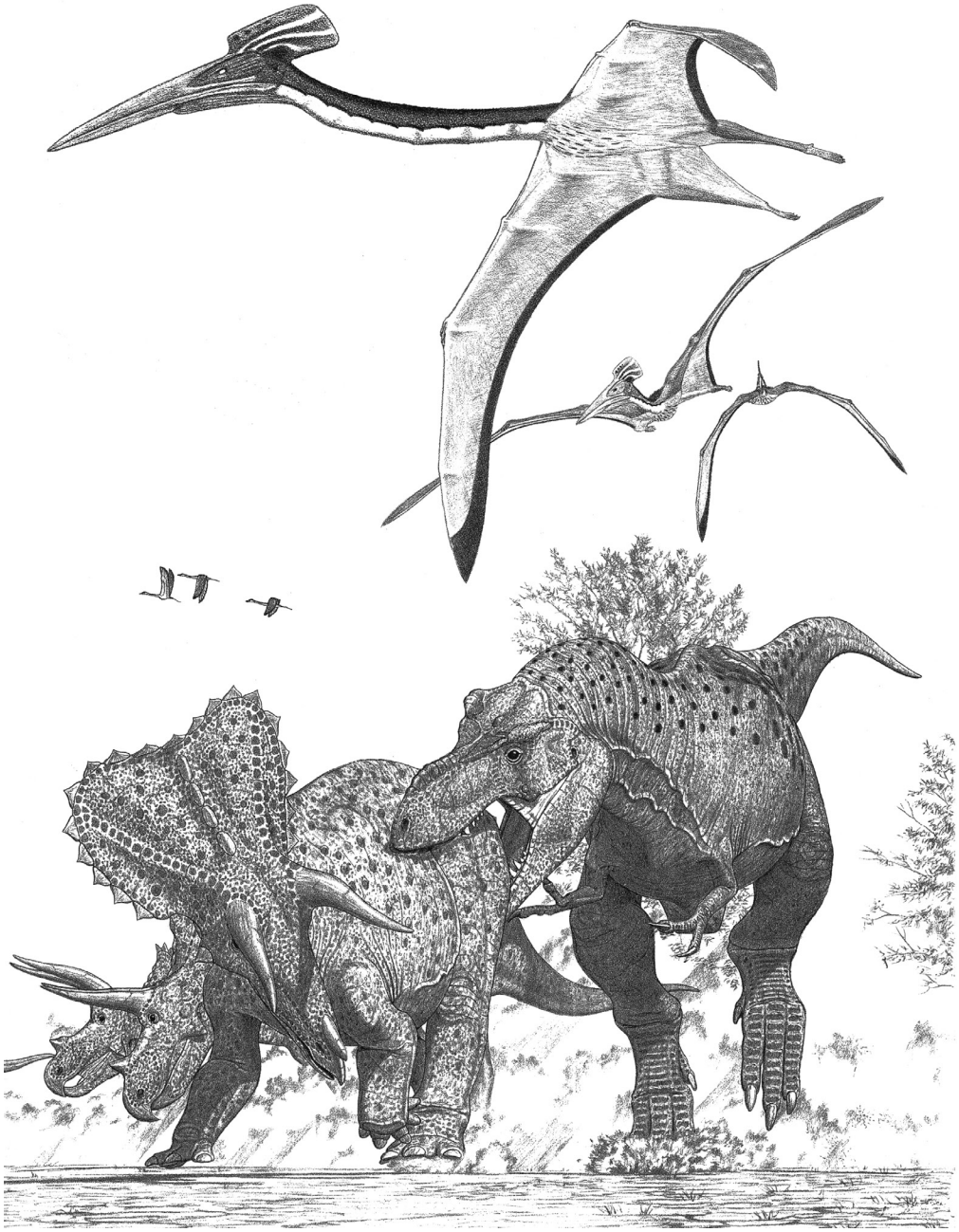
Although sauropods soon became limited to the titanosaurs, that group proliferated across most of the globe, being especially diverse in the Southern Hemisphere, wrapping up the 150 million years that made the clade the most successful herbivore group in Earth's history. Sauropods disappeared from North America for part of the Late Cretaceous, only to reappear in the drier regions toward the end. Some sauropods were armored; this may have in part been a means to protect the juveniles against the increasing threat posed by a growing assortment of predators. A few rather small titanosaurs had the short necks and square, broad mouths suited for grazing. Others were titanic, exceeding 50 and reaching perhaps 200 tonnes—as big as the biggest whales—up to the end of the dinosaur era. That indicates that some sauropods were as massive as and much longer than the greatest titans of the seas for 90 million years. Titanosaurs, supersized and otherwise, were subject to attack from abelisaur and allosauroid theropods, some of the latter matching bull elephants in bulk. This occurred until the allosauroids went out of existence in the early Late Cretaceous; why is not apparent. Perhaps even larger were the African sail-backed spinosaurs of the early Late Cretaceous; this group too did not make it to the end of the Mesozoic for mysterious reasons. Claims that the last spinosaurs were as aquatic as modern crocodilians are excessive.

The ultrawide-bodied ankylosaurs continued their success, especially in the Northern Hemisphere. One group of the armored herbivores developed tail clubs with which to deter and if necessary damage their meat-craving enemies, as well as settle breeding and perhaps feeding disputes within the species. The clubless nodosaurids also persisted. The iguanodonts faded from the scene to be replaced by their fleeter descendants, the duck-billed hadrosaurs, which evolved the most complex grinding dental batteries among dinosaurs and had elaborate head crests that identified the variety of species. The most common herbivores in much of the Northern Hemisphere, hadrosaurs may have been adapted in part to browse on the flowering shrubs and ground cover that were beginning to replace the fern prairies as well as to invade forest floors. Small ornithopods, not all that different from the bipedal ornithischians that had appeared back near the origins of the dinosaurs, continued to dwell over much of the globe. In the Northern Hemisphere the protoceratopsids, small in body and big in head, were common in many locales. It was from this stock that some of the most spectacular dinosaurs evolved—the rhino- and elephant-sized ceratopsids whose oversized heads sported horns, neck frills, great parrotlike beaks, and slicing dental batteries. These remarkable dinosaurs flourished for just the last 15 million years of the dinosaur era, limited largely to the modest-sized stretch of North America that lay west of the interior seaway; for some reason their presence in Asia was very restricted.

Birds, some still toothed, most belonging to the then abundant enantiornithines, others representing the beginnings of modern birds, continued to thrive. One group of oceanic birds lost flight to the point that they evolved into fully marine divers, rendering them the first fully oceanic dinosaurs. By the Late Cretaceous the classic short-armed coelurosaurs were no longer extant. The small predatory theropods consisted of the intelligent and sickle-clawed swift troodonts and leaping dromaeosaurs, some of which were still able to fly. One dromaeosaur group, the newly found halszkaraptors, lost their rod-stiffened tails seemingly in favor of a more watery life pursuing prey with duck-like snouts. Also successful were the short-tailed nonpredatory aveairfoilans, those being the deep-headed omnivorous oviraptorosaurs, many exhibiting dramatic head crests, as well as the small-headed, big-clawed herbivorous therizinosaurs. In both groups some species became quite large, as did some ornithomimosaurs. But among the latter group, the long- and slender-legged ornithomimids with their oversized hips became perhaps the fastest of all

dinosaurs—the fleetest modern ratites perhaps excepted—although they were closely matched by the colonial bug-eating alvarezsaurs, which when not dashing hither and yon used their short and amazingly stout arms and reinforced hands to break into insect nests.

Culminating more than 150 million years of big avepod history were the great tyrannosaurids, the most sophisticated and powerful of the gigantic predators. The classic tyrannosaurs came into existence only some 15 million years before the end of the Mesozoic and were limited to Asia and North America. Apparently they wandered, along with other theropods, hadrosaurs, and ankylosaurs, back and forth across the subpolar Bering land bridge, where some became specialized for the sharp winter climate. Farther south in central Asia, more temperate climes included winter snows. In North America a size race occurred as tyrannosaurids, ceratopsids, nodosaurids, ankylosaurids, and pachycephalosaurids reached unprecedented sizes for their groups in the final few million years of the Cretaceous, resulting in the classic *Tyrannosaurus*, *Triceratops*, *Ankylosaurus*, and *Pachycephalosaurus* fauna; the edmontosaur hadrosaurs got bigger too. This may have been the result of a predator-prey arms race, or expansion of the resource base as the retreating interior seaway linked the eastern and western halves of the continent into a larger land area, or a combination of both. Nodosaurs may have been the first of the ankylosaurs to get really big, followed by the ankylosaurids. Not getting larger



Latest Cretaceous *Tyrannosaurus imperator*, *Triceratops horridus*, and *Quetzalcoatlus*

were ornithomimids, some of which were actually small. And the very last edmontosaurs may not have been the very biggest. While some edmontosaurs evolved unusually long and broad duck bills especially well suited for grazing ground cover, they may not have made it as far in time as less-extreme-beaked relations.

It is interesting that the scrappy titanosaur remains from the latest Mesozoic, which may represent the largest land animals known to date, are from India. Although India was its own modest-sized subcontinent tectonically, sailing north as it helped close off the Tethys Ocean, it could have supported a population of super land giants. By the end of the Cretaceous the continents had moved far enough that the world was assuming its modern configuration. At the terminus of the period a burst of uplift and mountain building had helped drain many of the seaways, although Europe remained an island archipelago. Flowering plants were fast becoming an ever more important part of the flora, and the first hardwood trees—among them the plane tree commonly planted in cities—appeared near the end of the period and were evolving into the first large hardwood trees. Conifers remained dominant, however, including the classic moisture-loving, fast-spreading, rapidly growing redwoods, which reached towering heights as they do today. In South America the browsing pressure of the towering titanosaurs may have continued to encourage the evolution of the umbrella-topped monkey-puzzle araucarians. Classic rain forests, however, still did not exist. Grasses had evolved: they tended to be water-loving forms and did not yet form dry grassland prairies, except perhaps in India, where drier grasslands may have been appearing.

Then things went catastrophically wrong.

EXTINCTION

The mass extinction at the end of the Mesozoic is generally seen as the second most extensive in Earth's history, after the one that ended the Paleozoic. However, the earlier extinction did not entirely exterminate the major groups of large land animals. At the end of the Cretaceous all nonavian dinosaurs, the only major land animals, were lost, leaving only flying birds as survivors of the group. Among the birds, all the toothed forms, plus the major Mesozoic bird branch, the enantiornithines, as well as the flightless birds of the time, were also destroyed. So were the last of the superpterosaurs and the most gigantic of the crocodilians.

It is difficult to exaggerate how remarkable the loss of the dinosaurs was. If dinosaurs had repeatedly suffered the elimination of major groups and experienced occasional diversity squeezes in which the Dinosauria was reduced to a much smaller collection that then underwent another evolutionary radiation until the next squeeze, then their final loss would not be so surprising. But the opposite is the case. A group that had thrived for over 150 million years over the entire globe, rarely suffering the destruction of a major subgroup and usually building up diversity in form and species over time as it evolved increasing sophistication, was in short order completely expunged. The small dinosaurs went with the large ones, predators along with herbivores and omnivores, and intelligent ones along with those with reptilian brains. It is especially notable that even the gigantic dinosaurs did not suffer repeated extinction events. Sauropods were always a diverse and vital group for most of the reign of dinosaurs. The same was true for giant theropods once they appeared, as well as ankylosaurs and the iguanodonts/hadrosaurs. Only the stegosaurs had faded away well into the dinosaur era. In contrast, many of the groups of titanic Cenozoic mammals appeared, flourished relatively briefly, and then went extinct. Dinosaurs appear to have been highly resistant to large-scale extinction. Rendering their elimination still more remarkable is that one group of dinosaurs, the birds, did survive, as well as aquatic crocodilians, lizards, snakes—the latter had evolved by the Late Cretaceous—amphibians, and mammals that proved able to weather the same crisis.

It has been argued that dinosaurs were showing signs of being in trouble in the last few million years before the final extinction. Whether they were in decline has been difficult to verify or refute even in those few locations where the last stage of the dinosaur era was recorded in the geological record, such as western North America where the fossil data are the best. For example, western North American hadrosaurs sported an array of crested forms during the Campanian and early Maastrichtian, but by the end of the latter they were down to flat-skulled *Edmontosaurus*. Over the same period ceratopsids went from a diversity of centrosaurs and chasmosaurs to just one species of *Triceratops*. On the other hand, *Tyrannosaurus* seems to have gone from one species to two. That the big herbivore decline was not just a western North American thing is demonstrated by the apparent decline in the variety of dinosaurian eggs in China in the last two million years of the Mesozoic. Even if these declines did occur, they were modest, and other regions of the globe may not have seen a decrease. At the Cretaceous/Paleocene (K/Pg) boundary (formerly the Cretaceous/Tertiary [K/T] boundary), the total population of juvenile and adult dinosaurs should have roughly matched that of similar-sized land mammals before the advent of humans, numbering in the billions and spread among many dozens or a few hundred species on all continents and many islands.

A changing climate has often been offered as the cause of the dinosaurs' demise. But the *climatic* shifts at the end of the Cretaceous were neither strong nor greater than those already seen in the Mesozoic. And dinosaurs inhabited climates ranging from tropical deserts to icy winters, so yet another change in the weather should not have posed

such a lethal problem. If anything, reptiles should have been more affected. The rise of the flowering plants has been suggested to have adversely impacted dinosaurs, but the increase in food provided by the fast-growing seed- and fruit-producing plants appears to have been so beneficial that it spurred the evolution of late Mesozoic dinosaurs. Mammals consuming dinosaur eggs were another proposed agent. But dinosaurs had been losing eggs to mammals, and for that matter lizards and the like, for nearly 150 million years, and so had reptiles and birds without long-term ill effects. The spread of diseases as retreating seaways allowed once-isolated dinosaur faunas to intermix is not a sufficient explanation because of the prior failure of disease to crash the dinosaur population, which was too diverse to be destroyed by one or a few diseases and which would have developed resistance and recovered its numbers. Also unexplained is why other animals survived.

The solar system is a shooting gallery full of large rogue asteroids and comets that can create immense destruction. There is widespread agreement that the K/Pg extinction was caused largely or entirely by the impact of at least one meteorite, a mountain-sized object that fell from the northeast at a steep angle and formed a crater 180 km (over 100 mi) across, on the Yucatán Peninsula of Mexico. The evidence strongly supports the object being an asteroid rather than a comet, so speculations that a perturbation of the Oort cloud as the solar system traveled through the galaxy and its dark matter are at best problematic. The explosion of 100 teratons surpassed the power of the largest H-bomb detonation by a factor of 20 million and dwarfed the total firepower of the combined nuclear arsenals at the height of the Cold War. The blast and heat generated by the explosion wiped out the fauna in the surrounding vicinity, and enormous tsunamis, either arriving directly from the impact area, or locally induced by the massive worldwide earthquakes emanating from the massive hit, cleared off coastlines up what was left of the interior seaway, across the Atlantic and even the Pacific. The cloud of high-velocity debris ejected at near-orbital velocities into near space glowed hot as it reentered the atmosphere in the hours after the impact, creating a world-wrapping pyrosphere that may have been searing enough to bake animals to death as it ignited planetary wildfires. A fossil site exactly at the K/Pg divide in North Dakota appears to record some of these events, including remains of dinosaurs possibly drowned by local flooding, and impact debris in the gills of fish. The latter suggests it was a springtime disaster. The initial impact would have been followed by a solid dust pall that plunged the entire world into a dark, cold winter lasting for years, combined with severe air pollution and acid rain. As the aerial particulates settled, the climate then flipped as enormous amounts of carbon dioxide—released because the impact happened to hit a tropical marine carbonate platform and dug deeply into it at a steep angle (a more glancing impact or one elsewhere might not have had such serious effects)—created what some reconstruct as an extreme greenhouse effect that baked the planet for many thousands of years. Such a combination of agents appears to solve the mystery of the annihilation of the dinosaurs. The modern-style birds that got through, albeit barely, may have done so because they brooded their eggs, protecting them from the dreadful climate, and had flexible kinetic bills that aided feeding on whatever was left to eat. Even so, this scenario remains problematic.

As big as the asteroid was, it was the size of a mere mountain and was dwarfed by the planet it ran into. It is not certain whether the resulting pyrosphere was as planetarily lethal as some estimate. Even if it was, heavy storms covering a small percentage of the land surface should have shielded a few million square kilometers, in total equaling the size of India, creating numerous scattered refugia. In exposed locations, dinosaurs that happened to be in burrows, caves, or deep gorges, or in fresh waters not subject to big wave action, should have survived the pyrosphere like the lucky crocodilians and amphibians. So should many of the eggs buried in covered nests. Birds and amphibians, which are highly sensitive to environmental toxins, survived the acid rain and pollution. Because dinosaurs were rapidly reproducing "weed species" whose self-feeding young could survive without the care of the parents, at least some dinosaur populations should have made it through the crisis, as did some other animals, rapidly recolonizing the planet as it recovered. Recent work challenges the extremity of the asteroid winter and the following hothouse.

A major complicating factor is that massive volcanism occurred at the end of the Cretaceous as enormous lava flows covered 1.5 million square kilometers, a third of the Indian subcontinent. Had this not been going on, the extinction could be blamed on the impact, whereas if the latter had not occurred, then the volcanism could be charged. Nor is it likely that bouts of intense volcanics are a regular occurrence. As it is, the extinction waters are muddied—similar to how the atomic bombings of Japan and the massive Soviet attack at the same time mean that the surrender cannot simply be assigned to the former. It has been proposed that the massive air pollution produced from the repeated supereruptions of the Deccan Traps damaged the global ecosystem so severely in so many ways that dinosaur populations collapsed in a series of stages, perhaps spanning tens or hundreds of thousands of years. This hypothesis is intriguing because extreme volcanic activity was responsible for the great Permian-Triassic extinctions, and other infrequent mass eruptions appear to have caused serious losses. Although the K/Pg Deccan Traps were being extruded before the Yucatán impact and in the process were possibly degrading the global fauna and flora, evidence indicates that the impact—which generated earthquakes of magnitude 9 over most of the globe (11 on the exponential scale at the impact site)—may have greatly accelerated the frequency and scale of the eruptions. If this is correct, then the impact was responsible for the extinction not just via its immediate, short-term effects, but by sparking a level of extra intense supervolcanism that prevented the recovery of the dinosaurs.

It is also possible that the Yucatán impactor was part of an asteroid set that hit the planet repeatedly, further damaging the biosphere. Even so, the combined impact/volcanic hypothesis does not fully explain why dinosaurs failed to survive problems that other continental animals did.

Although extraterrestrial impact(s), perhaps indirectly linked with volcanism, is the leading explanation, the environmental mechanisms that destroyed all the nonflying dinosaurs while leaving many birds and other animals behind remain incompletely understood.

AFTER THE AGE OF DINOSAURS

Perhaps because trees were freed from chronic assault by multistory sauropods, dense forests, including rain forests, finally appeared. In the immediate wake of the extinction there were no large land animals, and only large freshwater crocodilians could make a living feeding on fish. The loss of dinosaurs led to a second, brief Age of Reptiles as superboa snakes as long as the biggest theropods and weighing over a tonne quickly evolved in the tropics, which also sported big freshwater turtles. By 40 million years ago, about 25 million years after the termination of large dinosaurs, some land and marine mammals were evolving into giants rivaling the latter. Among the survivors of the Dinosauria, a number of birds lost flight and became small and large land runners and marine swimmers. Fast-running ratites have proven able to make a fair go of it in the face of modern mammalian competition on continents. But the main story of Cenozoic dinosaurs was their governance of the daylight skies, while the night was dominated by mammalian fliers, the bats. The greatest success story of modern flying dinosaurs? The marvelous diversity and numbers of the little but sophisticated passerine songbirds that fill field guides.

BIOLOGY

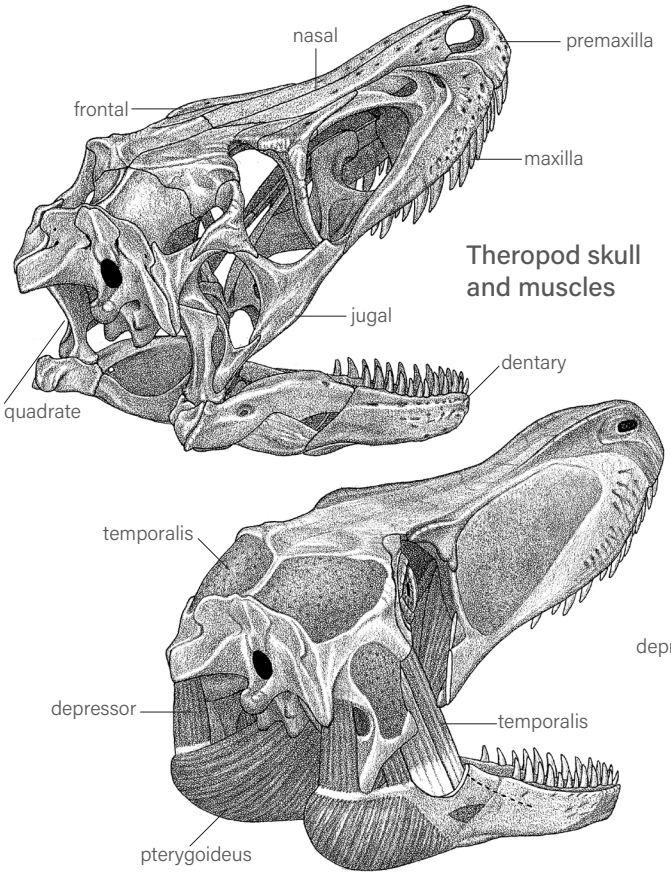
GENERAL ANATOMY AND LOCOMOTION

Dinosaur heads ranged from remarkably delicately constructed to massively built. In all examples the nasal passages or the sinuses or both were very well developed, a feature common to archosaurs in general. Many dinosaurs retained a large opening immediately in front of the orbits; in others this antorbital opening was almost entirely closed off. Unlike mammals with their extensive facial musculature, dinosaurs, like reptiles and birds, lacked facial muscles, so the skin was directly appressed to the skull. This feature makes dinosaur heads easier to restore than those of mammals. The external nares are always located far forward in the nasal depression no matter how far back on the skull the nasal openings extend. In some sauropods the nasal openings are set far back on the skull, above the eye sockets. It was once thought that this allowed these dinosaurs to snorkel when submerged. More recently it has been suggested that the retracted nostrils evolved to avoid irritation from needles as sauropods fed on conifers. Most conifers at that time, however, had soft leaves. In any case, the fleshy nostrils probably extended far forward so that the external nares were in the normal position near the tip of the snout. There is no anatomical evidence that any dinosaur had a proboscis. The skin covering the large openings in front of the orbits of many dinosaurs probably bulged gently outward, being filled with sinuses. Jaw muscles likewise bulged gently out of the skull openings aft of the eye sockets.

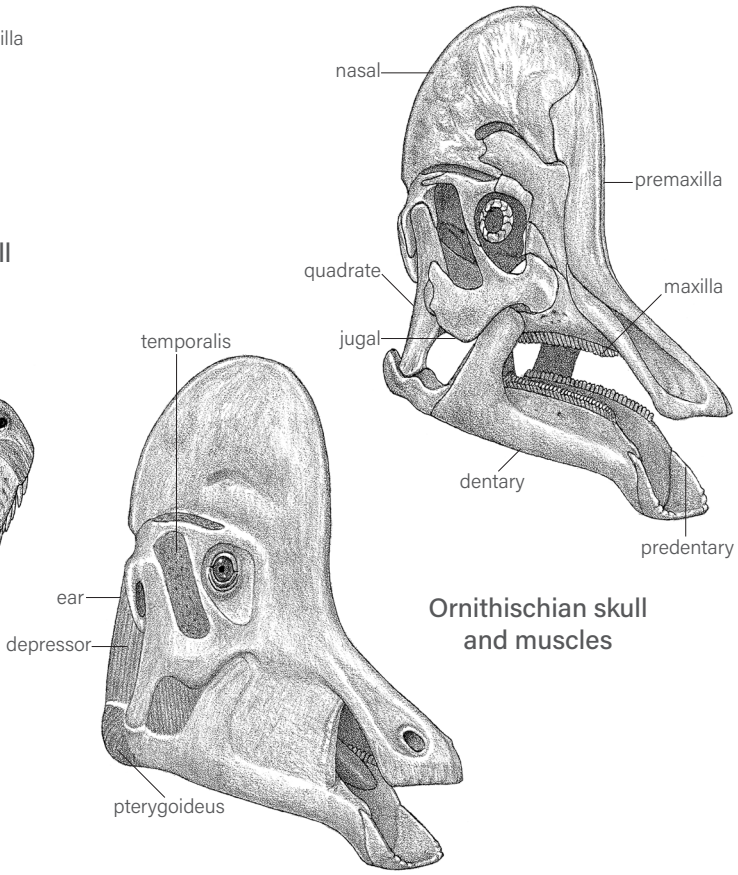
Among amphibians, tuataras, lizards, and snakes, the teeth tend to be set close to one another along fairly sharp-rimmed jaws, with the upper teeth always outside those on the lower jaw. The mouth is sealed and the teeth are covered by nonmuscular lips that cannot be pulled back to bare the teeth when the mouth opens. So even when the mouth is open, the teeth often remain entirely covered by lips, as well as gums; this is so in the biggest flesh-eating monitor lizards as well as herbivorous iguanas. This arrangement appears to be true of most theropods, and sauropods as well—one fossil of the latter appears to have a patch of lip tissue preserved astride some teeth. Thus the artistic tendency to show teeth entirely or partly exposed in theropods and sauropodomorphs may be an error as big as it is common. An exception among theropods would be the spinosaurs, which have a more crocodilian arrangement in which at least the front teeth are widely spaced in separate sockets on rounded jaw rims, with some lower teeth outside the uppers, so spinosaurs' snaggly front teeth may have been lipless and exposed when the jaws were closed. Some theropods and the ornithischians evolved beaks, and it has been suggested that prosauropods had incipient beaks. In ornithischians and therizinosaurs the beak was limited to the front of the mouth, but in some theropods and many birds, the beak displaces all the teeth. Beaked birds lack lips, and most do not have cheeks either. Condors, however, have short mouths because the sides of their jaws are covered by elastic cheek tissues, which differ from the muscular cheeks that cover the side teeth in many mammals. The side teeth of herbivorous prosauropods, the first sauropods, and ornithischians tend to be inset from the side of the mouth; the surrounding spaces are smooth surfaced, and the foramina that feed the soft tissue in the area of the mouth are reduced in number and enlarged in size, indicating that

well-developed, probably elastic cheeks covered some or all of the side teeth. Because the chewing dental batteries of many herbivorous dinosaurs were placed very close to one another to maximize the masticatory effect on plant material, cheeks were necessary to keep the bulk of the vegetation from falling out of the sides of the narrow mouth while the vegetation was being chomped down to smaller bits—herbivores with broad mouths that do not chew food, like plant-eating lizards, do not need such cheeks. Dinosaur cheeks were best developed in ornithischians, to the degree of being partly ossified into an plate of armor in some ankylosaurs, in which the cheeks extend all the way to the beak.

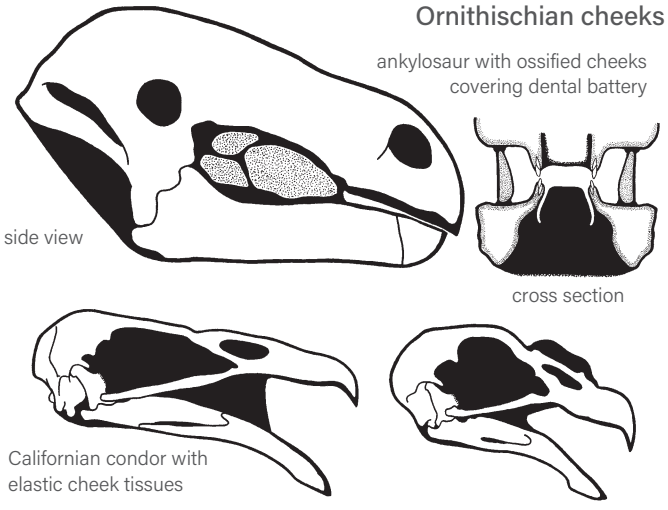
Set in sockets, all dinosaur teeth were constantly replaced through life in the manner of reptile teeth. Teeth ranged from blunt, leaf-shaped dentition suitable for crunching plants to serrated blades adapted to piercing and dicing flesh. Like the teeth of today's carnivores, those of predatory theropods were never razor sharp, as is often illogically claimed, because they would have injured the mouths they were in; one can run a finger firmly along the serrations

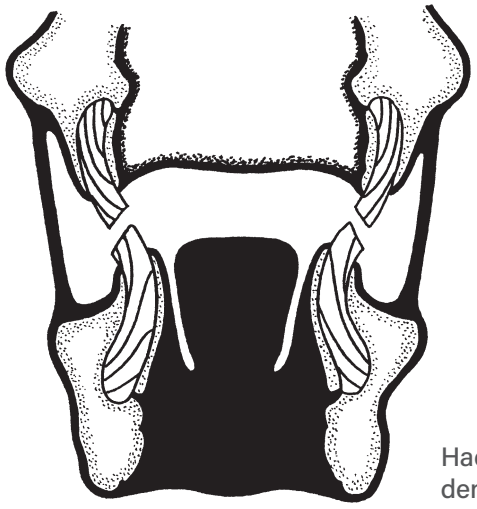


Theropod skull and muscles



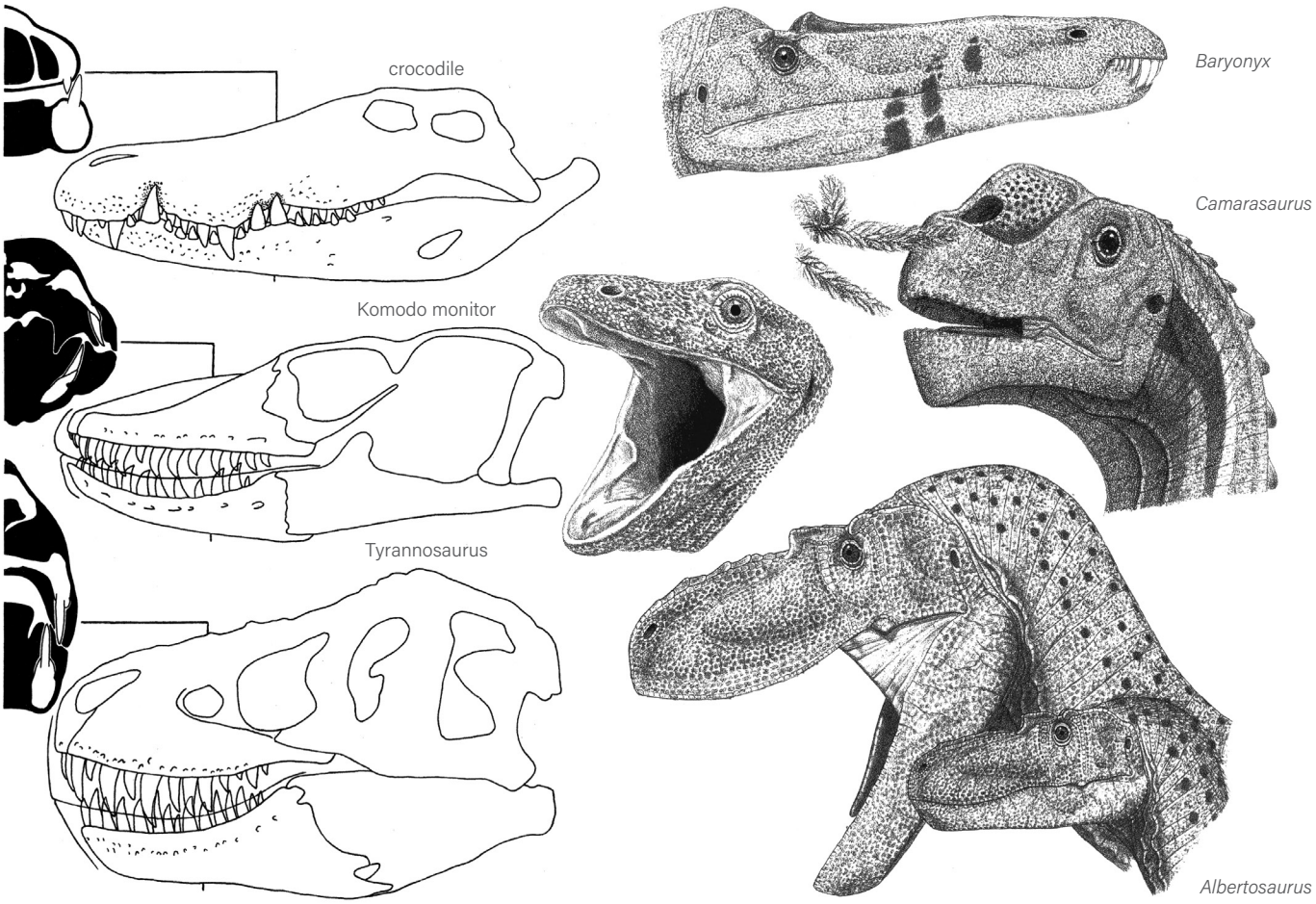
Ornithischian skull and muscles





Hadrosaur dental battery

Archosaur lip anatomy
based on X-rays



without harm. The teeth of iguanodonts and especially hadrosaurs and ceratopsids were concentrated into compact dental batteries made up of hundreds of teeth, although only a minority formed the plant-processing pavement at a given time. A few sauropods also evolved dental arrays with fast replacement, in their case at the front edge of the jaws where the teeth cropped plant material. Because dinosaurs were not lizards or snakes, they lacked flickering tongues. Dinosaurs had well-developed hyoids, suggesting that the tongues they supported were similarly developed. In predatory theropods the tongue was probably simple and inflexible. The tongues of herbivorous dinosaurs were likely to have been more supple and complex in order to help manipulate and, in the case of ornithischians, chew fodder.

In some large dinosaurs the eyes were in the upper part of the orbit. Bony sclerotic eye rings that helped support the large orbs often show the actual size of the eye both in total and indirectly in that the diameter of the inner ring tends to closely match the area of the visible eye when the eyelids are open. Most dinosaurs had large eyes, yet relative eye size decreases as animals get bigger. Although the eyes of giant theropods were very large, they looked small compared to the size of their heads. Even the eyes of ostriches, the biggest among living terrestrial animals, do not appear that large on the living bird. In the predatory daylight raptors, a bony bar running above the eyeball provides the fierce "eagle look." Interestingly, the flesh-eating theropods lacked this bar, but it was present in some of the smaller ornithischians, giving these plant eaters a more intimidating appearance than that of equally peaceful doe-eyed herbivorous mammals. The purpose of the eye bar is not well understood. It may shade the eyes from glare, it may strengthen the skull during feeding and chewing, and it may have helped protect the eyes of burrowing ornithopods from dirt and dust. Whether the pupils of dinosaur eyes were circular or slit shaped is not known. The latter are most common in nocturnal animals, and either may have been present in different species. The eyes of birds and reptiles are protected by both lids and a nictitating membrane, so the same was presumably true in dinosaurs.

The outer ear is a deep, rather small depression between the quadrate and jaw-closing muscles at the back of the head. The eardrum was set in the depression and was connected to the inner ear by a simple stapes rod. The orientation of the semicircular canals of the inner ears is being used to determine the posture of dinosaur heads. For

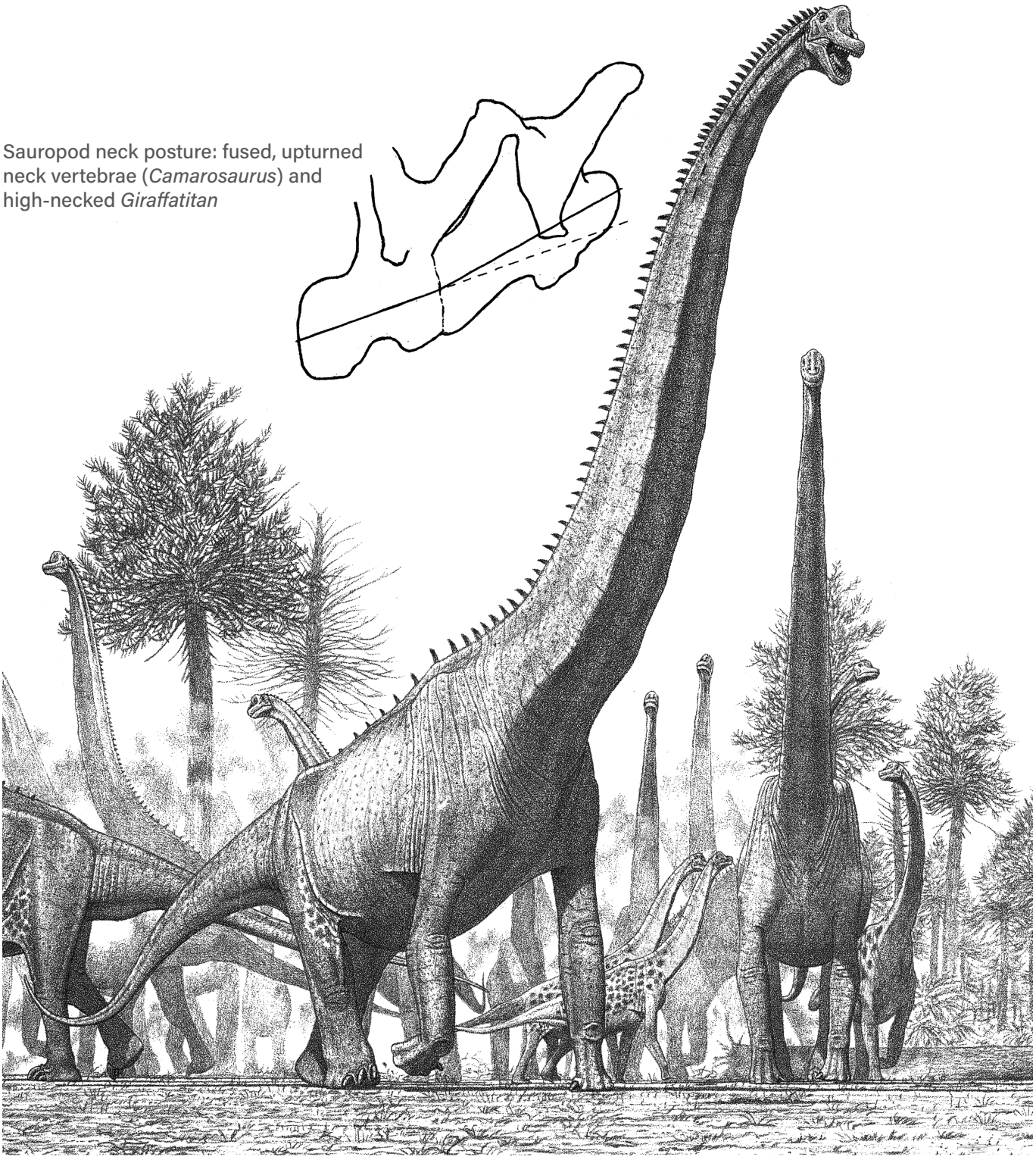
example, short-necked diplodocoid heads pointed straight down, according to this method, implying that they grazed ground cover. The situation may, however, be more complicated, reducing the reliability of this method. In living animals the relationship between the orientation of the semicircular canals and the normal carriage of the head is not all that uniform even between individuals of a species. That animals position their heads in different ways depending on what they are doing does not help. Giraffes feed with the head pointing straight down when browsing on low shrubs, or horizontally, or straight up when reaching as high as possible, so the orientation of the semicircular canals is not necessarily informative. It is widely thought that the broad-beaked, duck-billed hadrosaurs were grazers, so their heads should often have been directed straight down. Yet their semicircular canals favor a horizontal head posture. The semicircular canals of at least some prosauropods seem to show that they typically held the nose tilted somewhat upward, an odd pose not normal in large herbivores. It seems that the posture of the semicircular canals is determined at least in part by the orientation of the braincase with the rest of the skull and does not reflect the orientation of the head as well as has been thought.

Dinosaur necks were made up of just 7 to up to 19 vertebrae, with some birds having even more, compared to the 7 nearly all mammals have—in dinosaurs the first vertebra, the atlas, is very small. The necks of many dinosaurs tend to articulate in a birdlike S curve, as they do in most theropods and ornithopods. The beveling of the vertebrae is especially strong in some theropods. If anything, animals tend to hold their necks more erect than the articulations indicate. In other groups, such as ankylosaurs and ceratopsids, the necks were straighter. There has been a tendency to make dinosaur necks too short by placing the shoulder girdle too far forward. Even ankylosaur necks were long enough to accommodate two or three well-spaced armor rings. The flexibility of dinosaur necks ranged from low—the first few vertebrae of the short-necked ceratopsids were even fused together—to fairly high in longer-necked examples, but no dinosaur had the full set of special adaptations that make bird necks exceptionally mobile. What many dinosuars did have were overlapping neck ribs, with a slender tapering rod overlapping the next rib via a sliding articulation, a common archosaur feature retained in crocodilians. Presumably the overlap strengthened the neck without preventing flexion. The overlap was lost in a lot of dinosaurs including ornithomimids, most birdlike dinosaurs including birds themselves, most diplodocoid sauropods, and all the ornithischians, presumably as a means of further increasing neck flexibility.

The posture and function of the long necks of sauropods have become controversial. Some researchers propose a simplistic model in which the necks of all sauropods were held nearly straight and horizontally and, in a number of cases, could not be raised much above shoulder level. This was most true of one group, the short-necked diplodocoids. Otherwise the situation is complex and not well understood. Many of the sauropod necks that have been restored in a straight line show obvious misarticulations or are based on vertebrae that are too distorted and incomplete to be reliably articulated. The neck vertebrae of different giraffe individuals do not articulate consistently: they can range from arcing strongly downward in juveniles to being strongly erect in adults. This reflects the differing thickness of the cartilage pads between the vertebrae and demonstrates that cartilage as well as bones must be present to articulate necks properly. This is an obvious problem in that cartilage is rarely preserved in fossils. The well-preserved neck and trunk vertebrae of the prosauropod *Yizhousaurus* are so strongly wedge shaped that they describe an impossibly strong downward arc; in life, cartilage straightened that out. In many dinosaur skeletons the vertebrae are found jammed tightly together, probably because the intervening cartilage disks dried out after death and pulled the bones together.

In some articulated dinosaur skeletons, the vertebrae are still separated by the substantial gap that was filled by cartilage. The only example in which the cartilage between the vertebrae was preserved in a sauropod neck is two neck-base vertebrae of an old camarasaur that fused before death. Contrary to the prediction based on horizontal-necked sauropods, the vertebrae are flexed upward as though the neck was held well above shoulder level. Because sauropod necks had so many vertebrae, just 10 degrees of upward flexion between each pair allowed most sauropods to raise most of the neck nearly vertically, with the head far above shoulder level. Living ostriches and giraffes hold their necks at different angles depending on what they are doing, and it is possible that sauropods did not have specific neutral neck postures. There is no reason to assume that sauropods did not hold their necks higher than the bones may seem to indicate, and most researchers favor the probability that many sauropods regularly held their heads high.

Giraffe necks are not heavily muscled despite having solid vertebrae that have to support a large head. Sauropod necks held up much smaller heads and were highly pneumatic, so they should not have been heavily muscled either. In some sauropods tall shoulder spines indicate that a fairly deep set of nuchal ligaments and tendons helped support the neck. In a number of other sauropods the neural spines were doubled in order to improve neck support. The upper neck muscles of big-headed pachycephalosaurs and ceratopsians should have been powerfully built, and some ceratopsids had the tall shoulder withers that indicate the presence of deep nuchal tendons. Mummies show that the hadrosaurs, whose neck vertebrae appear slender relative to their rather large heads, had deep nuchal ligaments to help hold them up. The predatory theropods probably had the strongest neck muscles, which helped drive the teeth deeper into the flesh of their prey. Also powerful were the neck muscles that the ceratopsids used to wield their horns.



Sauropod neck posture: fused, upturned neck vertebrae (*Camarosaurus*) and high-necked *Giraffatitan*

With the dorsals and sacrals combined, the 15 to 27 trunk vertebrae of dinosaurs articulated either in a nearly straight line or, more often, in a dorsally convex arch that varied from subtle to very strong; swaybacks seem rare at best. The nature of the vertebral articulations, and in many cases ossified interspinal tendons, indicates that dinosaurs had stiffer backs than lizards, crocs, and most mammals, although the trunk vertebrae of dinosaurs were not normally fused the way they often are in birds. As in most vertebrates including lizards, crocodilians, and birds, the front ribs are strongly swept back in articulated dinosaur skeletons of all types; they are not vertical as they are in many mammals. Dinosaur belly ribs tend to be more vertical, but this condition is variable. As is typical of meat eaters,

the bellies and hips of the flesh-eating theropods were narrow, reflecting the small size of their digestive tracts as well as their athletic form. When they were hungry, the gut in front of the deep pelvis would have been somewhat hollowed out as in canids and cats on the hunt for flesh to gorge on and fill their highly expandable stomachs. Abdominal air sacs, if present, may have filled out some of the space of the gut even when the animals were hungry. The abdomens and hips of herbivorous dinosaurs were broader in order to accommodate more capacious digestive tracts.

Some plant-eating dinosaurs, therizinosaur theropods, titanosauriform sauropods, pachycephalosaurs, most stegosaurs, and especially ankylosaurs took the broadening of the belly and hips to an extreme that seems absurd in the fattest of the armored dinosaurs. The shoulder blades of ankylosaurs were even twisted along their long axis to fit onto the rapid shift from the narrow shoulders to the fat abdomen. Because dinosaur trunk vertebrae and ribs formed a short, fairly rigid body with the shoulder and hip girdles close together, the trunk musculature was rather light, like that of birds. Theropods and prosauropods retained gastralia, a series of flexible bony rods in the skin of the belly. Each segment of the gastralia was made of multiple pieces. This may have been necessary in prosauropods because they flexed their trunks while running on all fours. Theropods needed flexible gastralia because their bellies changed dramatically in size as they gorged and fasted between hunts. Big game–hunting predators, especially, bloated themselves after a kill and then fasted until the next one, so their bellies were hollow when they were on the hunt—this has been confirmed by the narrow articulated gastralia basket preserved with a tyrannosaur body that unlike most did not bloat up after death. In therizinosaurs the gastralia became more rigid, probably because these herbivores always kept their abdomens full of fermenting fodder. These structures were absent in sauropods and ornithischians, except for heterodontosaurs.

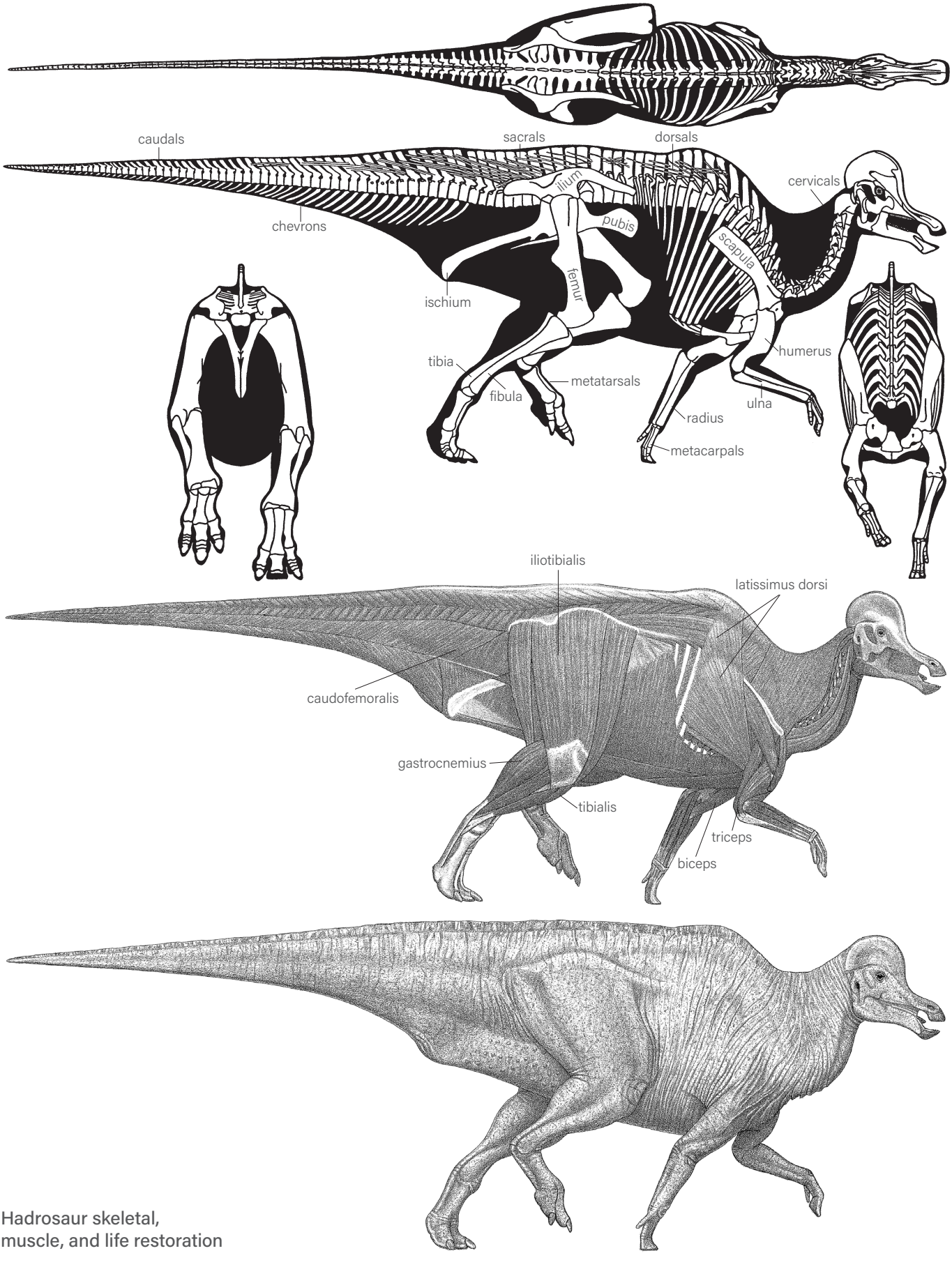
Consisting of 16 to 80 or so vertebrae, the tails of dinosaurs were highly flexible in most stegosaurs, theropods, and sauropodomorphs, especially the titanosaur sauropods, whose ball-and-socket joints may have allowed the tail to be arced directly over the back. In most of the sickle-clawed dromaeosaurid theropods, the club-tailed ankylosaurids, and ornithopods, part or all of the tail was stiffened to at least some degree by ossified tendons, with the tails of iguanodonts and hadrosaurs being especially inflexible.

In most dinosaurs the hip vertebrae and tail were in much the same line as the trunk vertebrae. Because tail drag marks are extremely rare at best among the immense number of trackways known for all the major dinosaur groups, the old-style convention of persistently tail-dragging dinosaurs cannot be correct. This is true even in those dinosaurs whose tail base was swept downward. That is why pretty much all the skeletons that were mounted that way have been reposed, and tails do not drag in modern dinosaur movies. In therizinosaurs and some sauropods, the hips and tail were flexed upward relative to the trunk vertebrae. This allowed the trunk to be held strongly pitched up while the hips and tail remained horizontal, increasing the vertical reach of the head while the dinosaur retained the ability to move on its hind legs. Because all dinosaurs bore most of their weight on their hind legs and usually had a long tail that acted as a counterweight to the body, all of them could rear up, even the few that had arms longer than their legs. Even small and medium-sized dinosaurs without caudal specializations may have been able to occasionally briefly bounce on their tail while lashing out with the hind limbs.

Many mammals can readily rotate their lower arm along its long axis to swivel the orientation of the hand, but others cannot do so as easily, if at all. Dinosaurs, including birds, are like the latter, although some flexibility may have been present in at least some cases. The wrist was mobile, in part to help the hand clear the ground during the forward stroke while walking or running. The simple wrists of some dinosaurs may seem to indicate a much stiffer joint, but this may reflect poor ossification of the wrist elements. In increasingly birdlike theropods the arm began to evolve the ability to fold up in order to tuck away large primary feathers, and to partly collapse the wing during aerial maneuvers, especially diving. This was facilitated by a large, half moon–shaped wrist carpal that acted as a hinge for the hand to swing back toward the lower arm. Wing folding did not become completely developed in nonavian dinosaurs.

Unlike many mammals, no dinosaur had hands that looked like its feet. The hands always lacked a heavy central pad, even in the giant quadrupeds. Sauropods, stegosaurs, iguanodonts, and hadrosaurs united their short fingers into a hoof-like hand by encasing them in single tight pad that barely showed the fingers, if at all. A very distinctive character of theropods, prosauropods, some sauropods, and some ornithischians was the big-clawed, inwardly directed thumb weapon, which could be held clear of the ground when walking with the arms. The palms of dinosaurs usually faced partly or strongly inward, especially in bipedal examples, but some trackways suggest this was not entirely universal. In some of the larger dinosaurs—iguanodonts and hadrosaurs, armored dinosaurs, ceratopsids, and sauropods—the hind feet were underlain by a large central pad similar to those of rhinos and elephants.

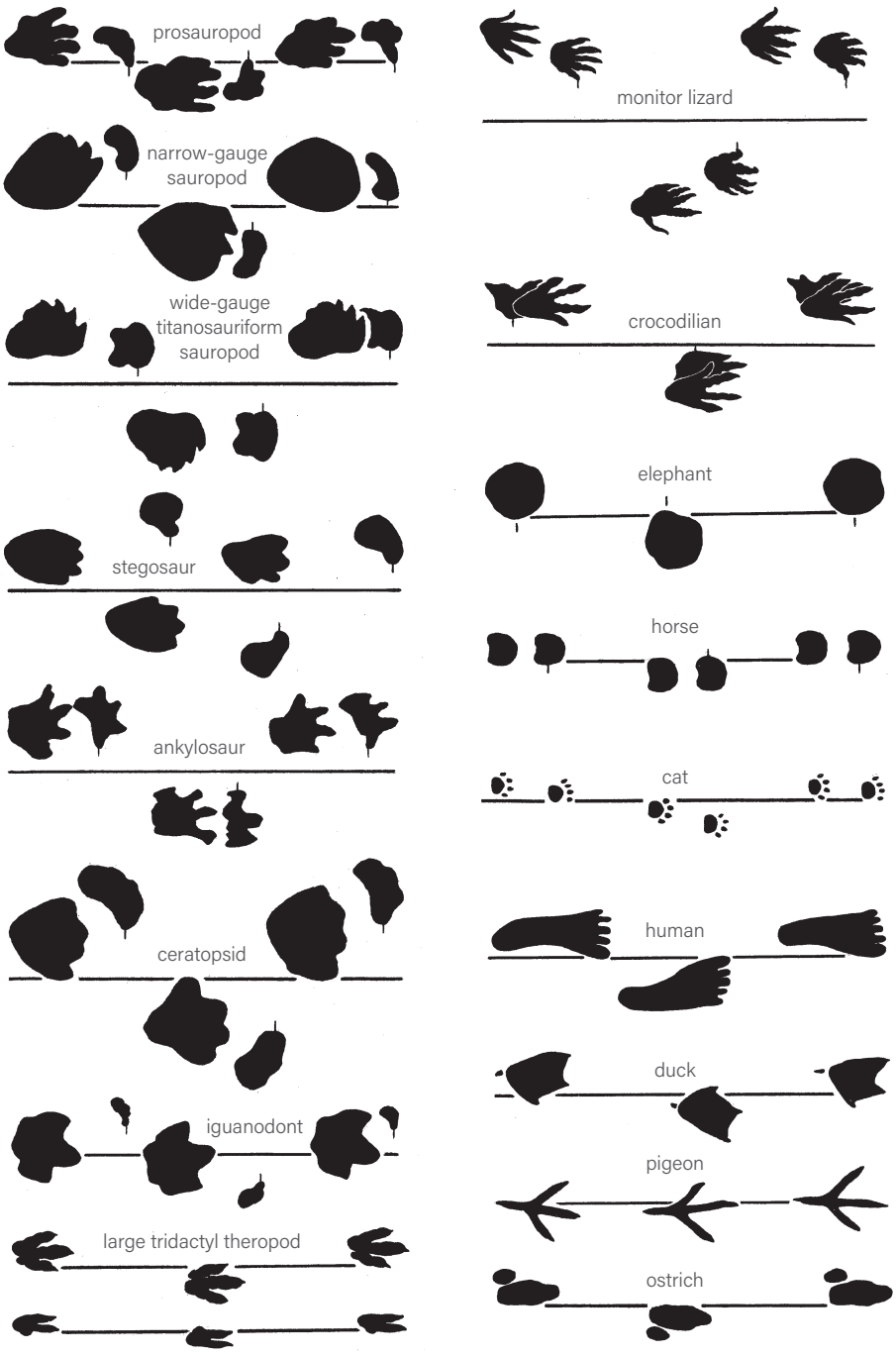
The front of the rib cage of quadrupedal dinosaurs was narrow from side to side in order to accommodate the shoulder girdle, both sides of which nearly met one another on the chest, and the shoulder joint was immediately in front of the rib cage. This differs from mammals, in which the shoulder joint is on the side of the chest. In theropods, including birds, the shoulder girdle is fixed in place, partly by a furcula that braces both scapula blades. Furculas are usually considered to be cofused clavicles, but they may instead be modified interclavicles that displaced the clavicles. Many reptiles and mammals have mobile shoulder girdles that help increase the stride length of the arms. This appears to have been true of quadrupedal dinosaurs because their clavicles are not fused



Hadrosaur skeletal,
muscle, and life restoration

as in many animals with mobile scapulas, or they do not contact one another, or they are lost. This is all the more likely in that the shoulder blades of four-legged dinosaurs resemble those of chameleons, which have highly mobile shoulders in side view; the scapula blade of most dinosaurs was subvertical as in most tetrapods, not horizontal. The exceptions are the most birdlike theropods and birds themselves, whose scapula blades are horizontal, in line with their being fliers.

In flying birds the shoulder joint faces sideways and upward so the arms can be held out to the side and raised vertically for flapping. In many predatory theropods the arms could also be swung laterally to grapple with prey. But even in winged protobirds like *Archaeopteryx* the arms could not be directed straight up. When dinosaurs were walking or running, trackways show that neither their arms nor legs were sprawled sideways like those of lizards. It is difficult to restore the precise posture of dinosaur limbs because in life the joints were formed by thick cartilage pads similar to those found on store-bought chickens, which are immature. Even so, some basics can be determined. The shoulder joints of quadrupedal dinosaurs faced downward and backward so that the arms could swing below the shoulder joints, and the cylindrical hip joints forced the legs to work below the hips. But this does not mean that the erect limbs worked in simple, entirely



Dinosaur and other trackways

vertical fore-and-aft planes. The elbows and knees, for instance, were bowed somewhat outward to clear the body, a feature common to many mammals as well. Trackways show that unlike the hands of mammals, which are often near the body midline when walking, the hands of dinosaurs were usually separated by at least two hand widths; the hands were rarely placed closer to the midline than the feet and were often farther from the midline than the feet. This was because the arms were oriented so that the hands were either directly beneath the shoulder joints or a little farther apart. The hind feet of dinosaurs often did fall on the midline, even among some of the largest quadrupeds, and were never separated by much more than the width of a single hind print, even among the broadest-hipped sauropods and armored dinosaurs. A notable exception to erect dinosaur legs is found in the small, early microraptorine dromaeosaurs. They sported extra wings on their hind limbs that in order to work required the legs to splay out to the sides. To do so, the femoral head was rounded and the hip socket partly closed off and more upwardly oriented than in the rest of the dinosaurs. This allowed the legs to operate in both the vertical and horizontal planes and in between. With no other dinosaurs having leg wings was this to be repeated.

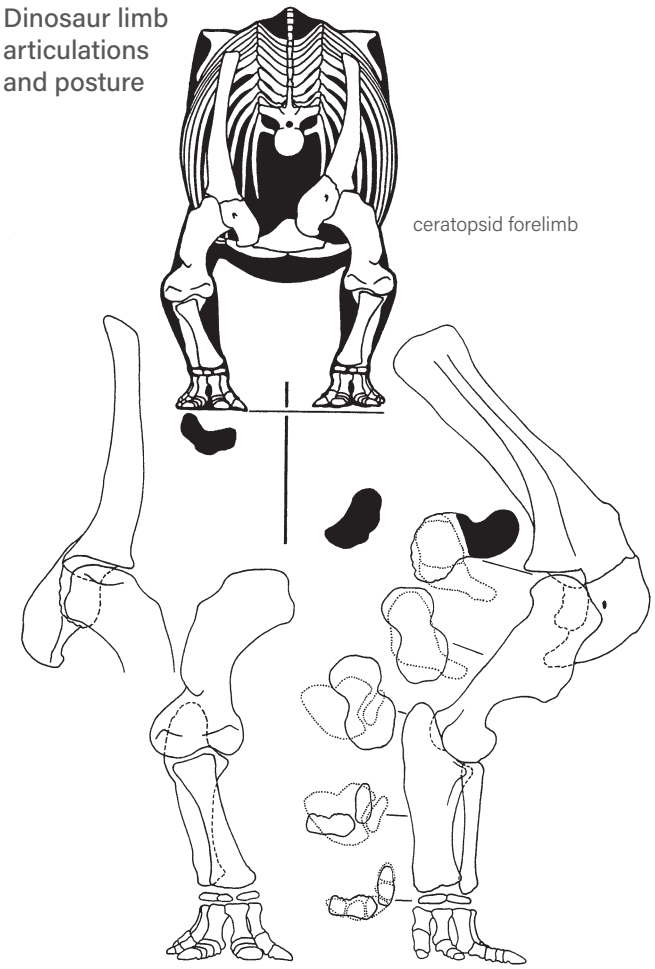
Dinosaur hands and feet were digitigrade, with the wrists and ankles held clear of the ground. Most dinosaurs had, like most terrestrial tetrapods, strongly flexed shoulder, elbow, hip, knee, and ankle joints that provided the springlike limb action needed to achieve a full run in which all feet were off the ground at some point in each complete step cycle. In addition, the ankle remained highly flexible, allowing the long foot to push the dinosaur into a ballistic stride. This was true of even the most gigantic theropods, ornithopods, ankylosaurs, and ceratopsids, which reached 5 to 15 tonnes. The knee joints of dinosaurs with flexed limbs were not fully articulated if they were straightened. Humans have vertical legs with straight knees because our vertical bodies place the center of gravity in line with the hip socket. In bipedal dinosaurs, because the head and body were held horizontally and were well forward of the hips, the center of gravity was ahead of the hip socket even with the long tail acting as a counterbalance, so the femur had to slope strongly forward to place the feet beneath the center of gravity. This arrangement is taken to an extreme in short-tailed birds, whose femur is nearly horizontal when they are walking in order to place the knees and feet far enough forward; when they are running, the femur of birds swings more strongly backward.

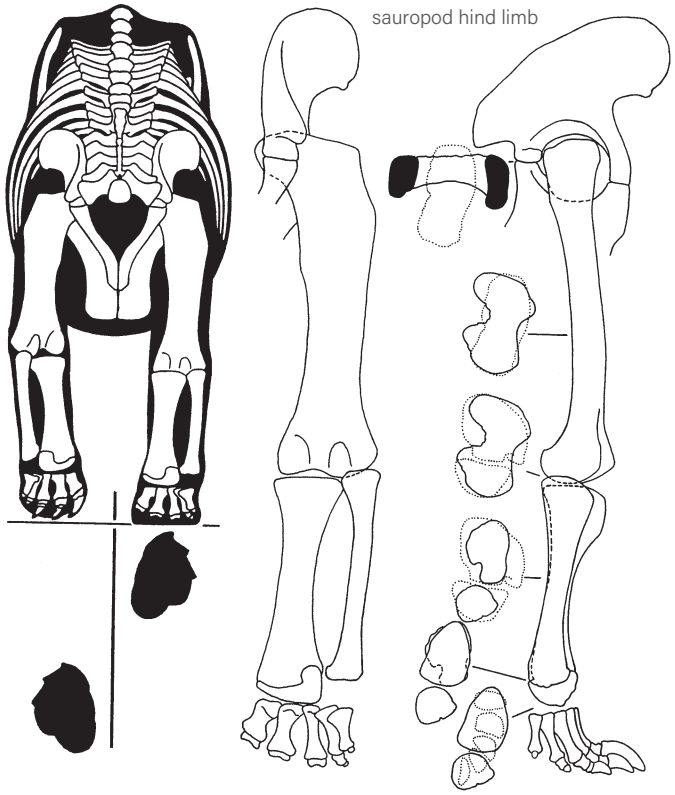
That dinosaurs normally retained thick cartilage pads in their limb joints throughout their entire lives, no matter how fast or big they became, is a poorly understood difference between them and adult birds and mammals, which have well-ossified limb joints. The manner in which dinosaurs grew up and matured may explain the divergence. In terms of locomotory performance it does not seem to have done dinosaurs any more harm than it does big running birds that still have cartilage joints when fully grown but not yet mature, and it may have had advantages in distributing weight and stress loads.

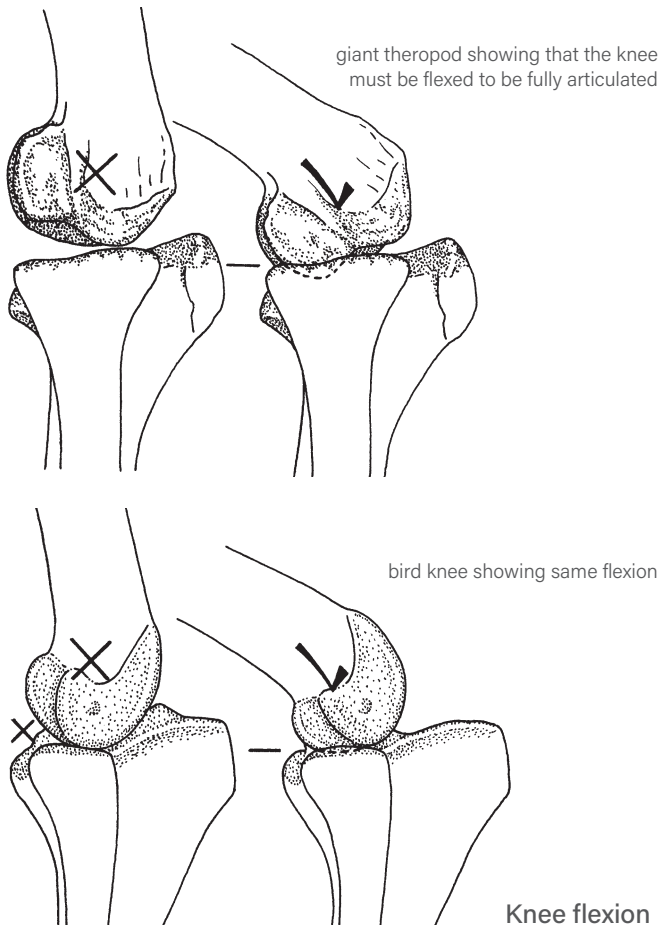
Two groups of dinosaurs, the stegosaurs and sauropods, evolved elephantine, more columnar, straighter-jointed limbs. The configuration of the knee was altered so that it remained fully articulated when straight. In addition, the ankle was less mobile, and the hind feet were very short. This suite of adaptations prevents the body from being propelled into a true run regardless of size: juvenile elephants cannot move any faster than their parents. Instead, at least one foot remains in contact with the ground at the highest speed.

The speed at which a fossil trackway was laid down can be approximated—with emphasis on approximated—by correlating the stride length of the trackway with the length of the articulated leg from the hip joint to the base of the foot. The latter can be estimated from the length of the foot; the ratio is four to one in a surprising array of animals—humans and theropods of all sizes and most types included. Mammals and birds of all sizes tend to walk at speeds of around 3–7 km/h (average 3 mph). Note that squirrels will bound rapidly, halt for a moment, then bound some more, stop, and so on. Humans and their dogs typically move at a similar overall pace, as do elephants. This is because the cost of locomotion per given distance scales closely to available aerobic power as size increases, so being big does not provide a major advantage. A typical walking speed recorded by trackways of tridactyl dinosaurs is around 5–7 km/h (4 mph).

The straight-limbed sauropods and stegosaurs should not have been able to move faster than elephants, which cannot exceed 25 km/h (15 mph). At the other end of the speed range, perhaps the fastest of dinosaurs are ostriches, which are credited with speeds of over 60 km/h (over 40 mph); among Mesozoic dinosaurs this may have been approached or matched by the ornithomimids. Adult animals do not burn lots of energy per unit time and exhaust themselves running about without a compelling reason, so it is not surprising that fossil speed trackways are scarce. The highest Cretaceous dinosaur land speed calculated so far is around 40–50 km/h (~30 mph), achieved by a 100 kg (200 lb) probable avepod. It is not a surprise that small and medium-sized dinosaurs with long, slender, flexed legs were able to run at speeds comparable to those of similar-sized ground birds and galloping mammals. Difficulties arise when trying to estimate the top speeds of flexed-limbed dinosaurs weighing many tonnes. Computer analysis has calculated that *Tyrannosaurus* could reach a top speed ranging from no better than that of a similar-sized elephant, 25 km/h (15 mph), up to the 40 km/h (25 mph) of a sprinting athlete. Because big-hipped, birdlike *Tyrannosaurus* was much better adapted for running than are elephants, and even by large avepod standards is exceptionally speed adapted with its enormous pelvis and running bird–like limbs, it is unlikely that it was as slow as proboscideans. Its anatomy is more in line with it being twice as fast or so as elephants, able to match galloping rhinos and approach nonthoroughbred horses. Lesser tyrannosaurids may have been a dash swifter than *Tyrannosaurus*, while







other, less speed-adapted, comparably titanic-sized avepods were likely to have been somewhat slower. The big horned dinosaurs should have been able to trot and perhaps gallop at velocities similar to those of rhinos of the same size. The bigger ornithopods look similarly capable.

Computer analyses are of limited use at best because they are hard pressed to fully simulate important aspects of animal locomotion, including the energy storage of prestretched elastic leg tendons and the resonant springlike effect of the torso and tail. Nor can computers successfully calculate the performance of extreme animals exemplified by the greatest of dinosaurs, the supersauropods that appear to have exceeded 100 tonnes, or how they managed to even stand upright much less move their whale-sized bodies on land as trackways show that they did. They appear no better proportioned to support their mass than are the already slow-moving elephants, which are 10 or more times smaller. Did the supersauropods not need "super" adaptations beyond those seen in elephants to move about the Mesozoic landscape, or did special adaptations such as stronger muscle fibers and pretensed tendons evolve to solve the problem? If the latter was true, then giant running dinosaurs may have used special adaptations to move faster than our computer models are indicating. Consider that if marine mammals were known only from fossils, it would be logical to conclude that no endotherms with

high metabolic rates would have been able to hold their breath long enough to dive very deep into high-pressure water that would certainly have killed them, and computer simulations would be cited as confirmation of that probable fact. Yet some whales and seals can dive thousands of meters because of physiological adaptations not preserved in fossils. The core and unavoidable problem with simulations is that they are simulating a simulation, not observing the actual performance of a living animal, so the results are no better than what was put into them and may not reproduce the actual parameters of a living creature. The outcomes can never be scientifically tested and verified.

An important aspect of assessing dinosaur speed and power is the mass of the limb muscles, which tend to make up a larger percentage of the total mass in fast runners than in slower animals. Because the muscles are not preserved in dinosaur fossils, it is not possible to accurately restore the speed of a given dinosaur—at best it can only be approximated. The exceptionally complex limb muscles of living mammals are the heritage of the unusual history of the early members of the group. Dinosaurs retained the simpler muscle patterns of reptiles, which are still seen in birds. A major muscle present in most reptiles and dinosaurs to varying degrees depending on the size of the tail base, but not in short-tailed birds and mammals, was the big caudofemoralis, which helps pull the hind limb back during the propulsive stroke.

Although the absolute size of dinosaur muscles cannot be exactly determined, their relative size among the different groups can be approximated. In reptile hips the ilium is so short that the thigh muscles have to be narrow, limiting their size. The much longer pelvic ilia of birds and mammals anchor a broad and powerful set of thigh muscles. The ilium of the early herrerasaurs and prosauropods was short, so they must have had narrow thigh muscles. In other dinosaurs the ilium was longer and deeper, anchoring a larger set of thigh muscles able to generate more sustainable power. This trend was taken to an extreme in some dinosaurs. In the ostrich-like ornithomimids and tyrannosaurids, the oversized pelvis indicates the presence of exceptionally large leg muscles able to power high speeds. The ceratopsid dinosaurs had even longer hips, which probably supported the big leg muscles required to propel the fast charges needed to fend off the similarly strong-muscled tyrannosaurs. It is interesting that the enormous sauropods did not have especially large ilia because they did not need large muscles to move at a fast pace. The same is true of elephants, which also lack large muscles below the knees because the feet that the shank muscles help operate are very short and nearly immobile. A similar situation was true of sauropods and stegosaurs. Faster animals have a large bundle of shank muscles that operate the long, mobile foot via long tendons. In bipedal dinosaurs, including birds, the large, drumstick-shaped collection of muscles below the knee is anchored on the cnemial crest projecting forward of the knee joint.

Fossil burrows indicate that some small dinosaurs dug burrows. This explains why small, bipedal ornithischians often had oversized shoulder girdles—they anchored the powerful upper arm muscles needed for digging with their broad hands. Any small dinosaur, juveniles of big species included, had the potential to burrow, but how many did so is not known.

Restorations of dinosaurs commonly simplify their surface contours, making their necks, tails, and legs into rather simple tubes and smoothing over the topography of the body. In sauropods the bulge of each neck vertebra was probably visible on the side of the neck, as it is in giraffes when viewed from the front—the speckled pattern of the fur hides that in side view. Because the trachea and esophagus of sauropods were probably tucked up between their cervical ribs, the bottom of their necks should have been fairly flat, unlike giraffe necks, which lack well-developed neck ribs. The upper muscles that hold the head and neck up are stronger than those that lower them, and the former formed a subtle bulging contour over the latter that ran the length of dinosaurs' necks. In dinosaurs with large arms, the upper end of the humerus bulged out a little, and in many but not all dinosaurs, a very large crest of the humerus formed a prominent contour along the upper front edge of the arm. The elbow joint formed a large bulge in front view, especially in the dinosaurs with massive arms—the ceratopsids, armored dinosaurs, and diplodocoids. The upper edge of the ilium was visible in living dinosaurs, especially the herbivores, in the same way that the pelvic bones of a cow can be seen under the skin.

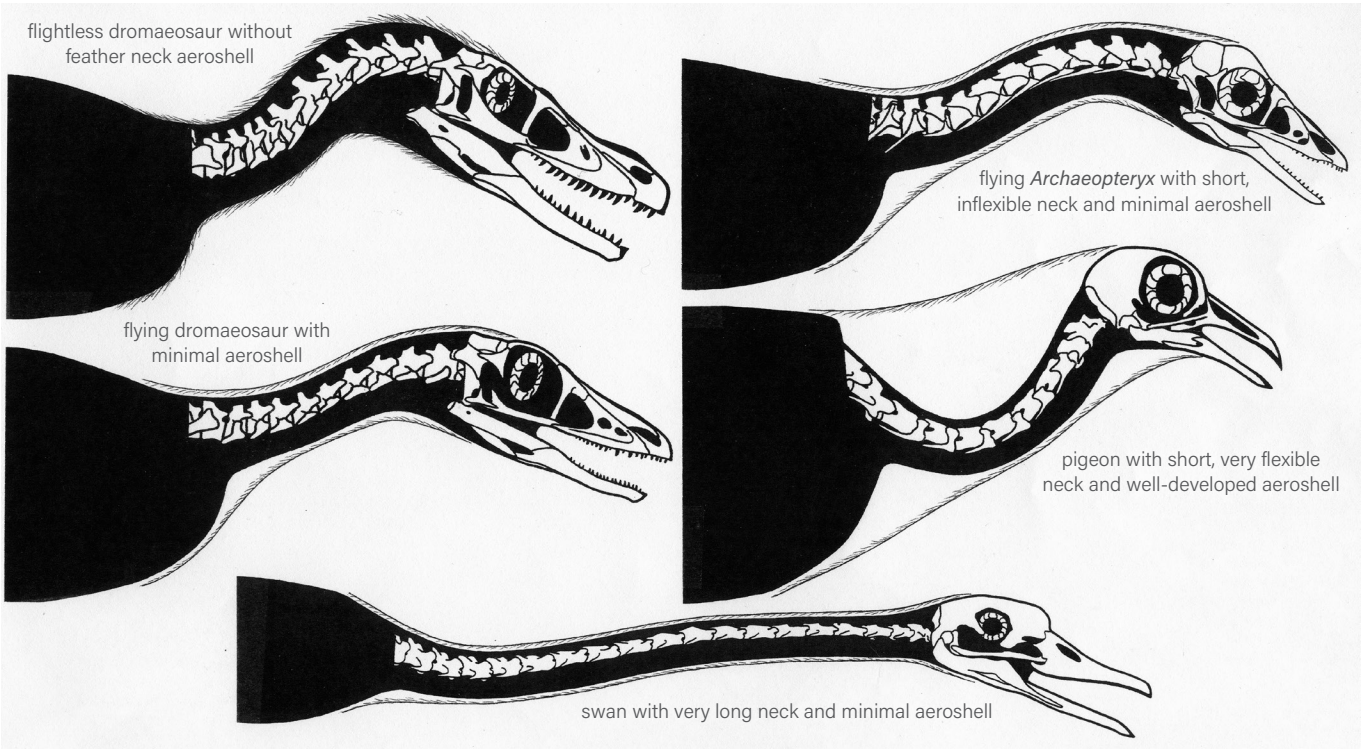
SKIN, FEATHERS, AND COLOR

Most dinosaurs are known from their bones alone, but we know a surprising amount about dinosaur body coverings from a rapidly growing collection of fossils that record their integument. It has long been known that large, and some small, dinosaurs were covered with mosaic-patterned scales. These can be preserved as impressions in the sediments before the skin rotted away, but in numerous cases traces of keratin are still preserved. Footprints sometimes preserve the shape of the bottom scales as well as the foot pads. The large dinosaurs whose skin is best known are the duck-billed hadrosaurs, for which some almost complete "mummies" are known. Lizard-like overlapping scales were not common among dinosaurs, although scales like those on the tops of some bird feet may have been present in birdlike dinosaurs, and overlapping plates have been found along the tails of small ornithischians and perhaps elsewhere. Dinosaur mosaic scales were commonly semi-hexagonal in shape, with larger scales surrounded by a ring of smaller scales, forming rosettes that were themselves set in a sea of small scales. These scales were often flat, but some were more topographic, ranging from small beads on up. Because dinosaur scales were usually not large, they tend to disappear from visual resolution when viewed from a dozen feet or more away. However, in some cases the center scale in a rosette was a large, projecting, subconical

scale; these were often arranged in irregular rows. On a given dinosaur the size and pattern of the scales varied depending on their location. The most spectacular scales yet known are those that adorned *Triceratops*. As big as the palm of a large person's hand, they were strongly subconical and may have borne a large central bristle.

The midline backs of some dinosaurs were adorned with nonarmor display tissue. This took the form of large, prominent scales, spines, and segmented and smooth-edged frills. At least some psittacosaur tails were adorned with a comblike set of very long bristles. In heterodontosaurs the dorsal bristles were denser and finer and ran along the back as well as the tail. Prominent skin folds like those seen on lizards are sometimes preserved and may have been fairly common in various dinosaurs. Soft crests, combs, dewlaps, wattles, and other soft display organs may have been more widespread than we realize. A pelican-like throat pouch has been found under the jaws of an ornithomimosaur theropod, and the throat pouches of stegosaurs and ankylosaurs, which started at the front of the lower jaws, were armored with a dense pavement of small ossicles. Armor plates were covered with hard keratin; an ankylosaur with the sheaths preserved shows that they were enlarged by a depth of about a third. Also lengthened by keratin sheaths were beaks, horns, and claws; in a few cases these have been preserved. Keratin typically lengthens a bony horn core by a third up to twofold; I usually add half.

Until recently neither scales nor any other kind of body covering had been discovered on small ornithischians. This data gap has finally been dramatically reduced by the discovery of a fiber coat on two examples. Feathers have long been known on the fossils of birds preserved in fine-grained lake or lagoon bottom sediments, including winged *Archaeopteryx*. After a fossil drought that lasted until the end of the last century, in the last three decades a growing array of small theropod dinosaurs, flightless and winged, have been found covered with bristle protofeathers or fully developed pennaceous feathers in the Yixian-Jiufotang beds. Some researchers have claimed that the simpler bristles are really degraded internal collagen fibers. This idea is untenable for a number of reasons, including the discovery of pigmentation—either visible to the naked eye or in microscopic capsules—in the fibers that allows their actual color to be approximated. Some small nonflying theropods also had scales at least on the tail and perhaps legs, and some small ornithischians such as psittacosaurs were largely scale covered. This suggests that the body covering of small dinosaurs was variable—ostriches lack feathers on the legs, and a number of mammals from a small bat through a number of suids as well as humans, rhinos, and elephants are essentially naked. Such variability even within a species may explain the apparently naked, isolated leg of a small ornithopod. Ironically, some paleoartists are going too far with feathering dinosaurs, giving many the fully developed aeroshells in which contour feathers streamline the head, neck, and body of most flying birds. But most Mesozoic dinosaurs did not fly, and like those birds whose ancestors lost flight long ago, flightless dinosaurs would have had shaggier, irregular coats for purposes of insulation and display. Also, modern birds have the hyperflexible necks that allow many but not all fliers to strongly U-curve the neck to the point that the head and heavily feathered neck



aerodynamically merge with the body. Dinosaurs and even early-flying dinobirds like *Archaeopteryx* and microraptors could not do this, so their less flexible necks stuck out ahead of the shoulders like those of a number of modern long-necked flying birds.

Because fibers covered basal ornithischians in addition to avepods, it is a good scientific bet that dinosaur insulation evolved once, in which case they were all protofeathers. The absence to date of protofeathers in Triassic and Early Jurassic protodinosaurs and basal dinosaurs is the kind of negative evidence that is no more meaningful than their lack of fossil scales, the kind that long led to the denial of insulation in any dinosaurs and is likely but not certainly to be settled by the eventual discovery of insulation in basal examples. However, it cannot be ruled out that insulation evolved more than once in dinosaurs. A question is why dinofur and feathers appeared in the first place. The first few bristles must have been too sparse to provide insulation, so their initial appearance should have been for nonthermoregulatory reasons. One highly plausible selective factor was display, as in the visually striking tail bristles of psittacosaurs. As the bristles increased in number and density to improve their display effect, they became thick enough to help retain the heat generated by the increasingly energetic archosaurs. The display-to-insulation hypothesis is supported by the fibers and feathers on some flightless dinosaurs such as heterodontosaurs functioning as both prominent display organs on some parts of the body and insulation cover on others.

A number of researchers argue that the pigment organelles of feathers preserve well, and their shape varies according to color, so they are being used to restore the actual colors of feathered dinosaurs. Although some researchers have challenged the reliability of this method, it appears to be sound, so this book uses the colors determined by this technique—doing so maximizes the probability of achieving correct coloration, whereas not doing so essentially ensures incorrect results. It appears that the feathers of some dinosaurs were, as might be expected, iridescent, using refraction rather than pigmentation to achieve certain color effects. There is no known method to restore the specific colors of scales, although differing degrees of shading can be assayed, and there is evidence that some dinosaurs were countershaded, being darker on top than below. The hypothesis offered by some researchers that the differing scale patterns on a particular dinosaur species correspond to differences in coloration is plausible, but some reptiles are uniformly colored regardless of variations in scales. Dinosaur scales were better suited to carry bold and colorful patterns like those of reptiles, birds, tigers, and giraffes than is the dull gray, nonscaly skin of big mammals, and the color vision of dinosaurs may have encouraged the evolution of colors for display and camouflage. Dinosaurs adapted to living in forested areas may have been prone to using greens as stealth coloring. On the other hand, big reptiles and birds tend to be earth tinged despite their color vision. Small dinosaurs are the best candidates for bright and/or bold color patterns like those of many but not all small lizards and birds. On yet another hand, because humans lack vision in the ultraviolet range, we miss seeing a lot of the coloration of many animals, so a number of reptiles and especially birds that look drab to us—including genders that look bland and much the same—feature dramatic ultraviolet color patterns, often for sexual purposes. Archosaurs of all sizes may have used specific color displays for intraspecific communication or for startling predators. Crests, frills, skin folds, and taller neural spines would be natural bases for vivid, even iridescent, display colors, especially in the breeding season. Because dinosaur eyes were bird- or reptile-like, not mammal-like, they lacked white surrounding the iris. Dinosaur eyes may have been solid black or brightly colored, like those of many reptiles and birds.

RESPIRATION AND CIRCULATION

The hearts of turtles, lizards, and snakes are three-chambered organs incapable of generating high blood pressures. The lungs, although large, are internally simple structures with limited ability to absorb oxygen and exhaust carbon dioxide and are operated by rib action. Even so, at least some lizards apparently have unidirectional airflow in much of their lungs, which aids oxygen extraction. Crocodilian hearts are incipiently four chambered but are still low pressure. Their lungs are internally dead-end, but they too seem to have unidirectional airflow, and the method by which they are ventilated is sophisticated. Muscles attached to the pelvis pull on the liver, which spans the full height and breadth of the rib cage, to expand the lungs. This action is facilitated by an unusually smooth ceiling of the rib cage that allows the liver to easily glide back and forth, the presence of a rib-free lumbar region immediately ahead of the pelvis, and, at least in advanced crocodilians, a very unusual mobile pubis in the pelvis that enhances the action of the muscles attached to it.

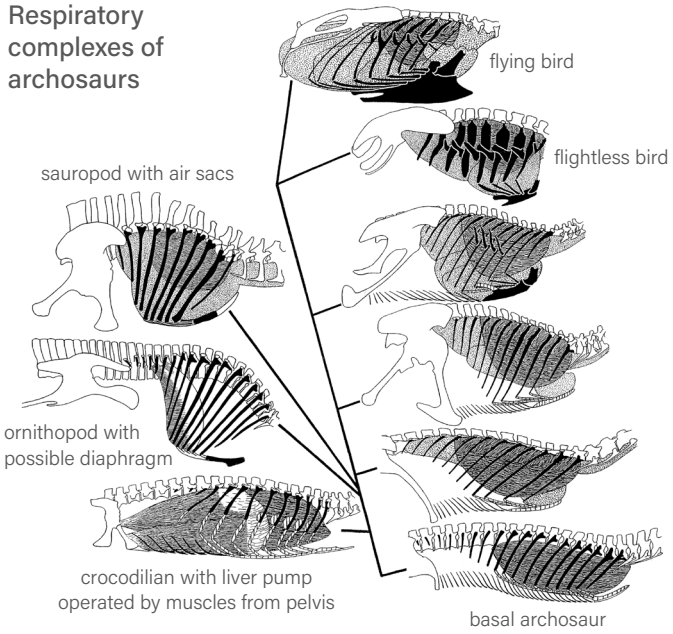
Birds and mammals have fully developed four-chambered, double-pump hearts able to propel blood in large volumes at high pressures. Mammals retain fairly large dead-end lungs, but they are internally very intricate, greatly expanding the gas-exchange surface area, and so are efficient despite the absence of one-way airflow. The lungs are operated by a combination of rib action and the vertical, muscular diaphragm. The presence of the diaphragm is indicated by the existence of a well-developed, rib-free lumbar region, preceded by a steeply plunging border to the rib cage on which the vertical diaphragm is stretched.

It is widely agreed that all dinosaurs probably had fully four-chambered, high-capacity, high-pressure hearts. Their respiratory complexes appear to have been much more diverse.

It is difficult to reconstruct the respiratory systems of ornithischians because they left no living descendants, and because their rib cages differ not only from those of all

living tetrapods but among different ornithischian groups. It is not possible to determine the complexity of their lungs; it can only be said that if ornithischians had high aerobic capacity, then their lungs should have been internally intricate. Because no ornithischian shows evidence of pneumatic bones, it can be assumed that they retained high-volume lungs that were either dead-end or had minor extensions similar to those in some reptiles, although airflow may have been partly unidirectional. Nor were their ribs highly mobile—in ankylosaurs most of the ribs were actually fused to the vertebrae. The belly ribs of ceratopsids were packed tightly together and attached to the pelvis, so they could not move either. It can be speculated that in most ornithischians abdominal muscles anchored on the ventral pelvis were used to push the viscera forward, expelling stale air from the lungs; when the muscles were relaxed the lungs expanded. One group of ornithischians had a different arrangement. In ornithopods there was a large rib-free lumbar region with a steeply plunging rib cage immediately ahead. This is so similar to the mammalian lumbar region that it is probable that a diaphragm, perhaps muscular, had evolved in the group. Peculiar among ornithischians are the heterodontosaurs, which had larger than usual, elongated sternals connected to the ribs by robustly constructed sternal ribs, and oddest of all, gastralia not otherwise seen in the Ornithischia. Presumably this means heterodontosaur breathing was distinct from that of other ornithischians, but exactly how is a mystery.

Restoring the respiratory complexes of saurischians, especially theropods, is much more straightforward because birds are living members of the group and retain the basic theropod system. Birds have the most complex and efficient respiratory system of any vertebrate. Because the lungs are rather small, the chest ribs that encase them are fairly short, but the lungs are internally intricate and have a very large gas-exchange area. The lungs are also rather stiff and set deeply up into the strongly corrugated ceiling of the rib cage. The lungs do not dead-end; instead, they are connected to a large complex of air sacs whose flexibility and especially volume greatly exceed those of the lungs. Some of the air sacs invade the pneumatic vertebrae and other bones, but the largest sacs line the sides of the trunk; in most birds the latter air sacs extend all the way back to the pelvis, but in some, especially flightless examples, they are limited to the rib cage. The chest and abdominal sacs are operated in part by the ribs; the belly ribs tend to be extra long in birds that have well-developed abdominal air sacs. All the ribs are highly mobile because they attach to the trunk vertebrae via well-developed hinge articulations. The hinging is oriented so that the ribs swing outward as they swing backward, inflating the air sacs within the rib cage, and then deflating the sacs as they swing forward and inward. In most birds the movement of the ribs is enhanced by ossified uncinate processes that form a series along the side of the rib cage. Each uncinate process acts as a lever for the muscles that operate the rib the process



is attached to. In most birds the big sternal plate also helps ventilate the air sacs. The sternum is attached to the ribs via ossified sternal ribs that allow the plate to act as a bellows on the ventral air sacs. In those birds with short sternums, the flightless ratites, and in active juveniles, the sternum is a less important part of the ventilation system.

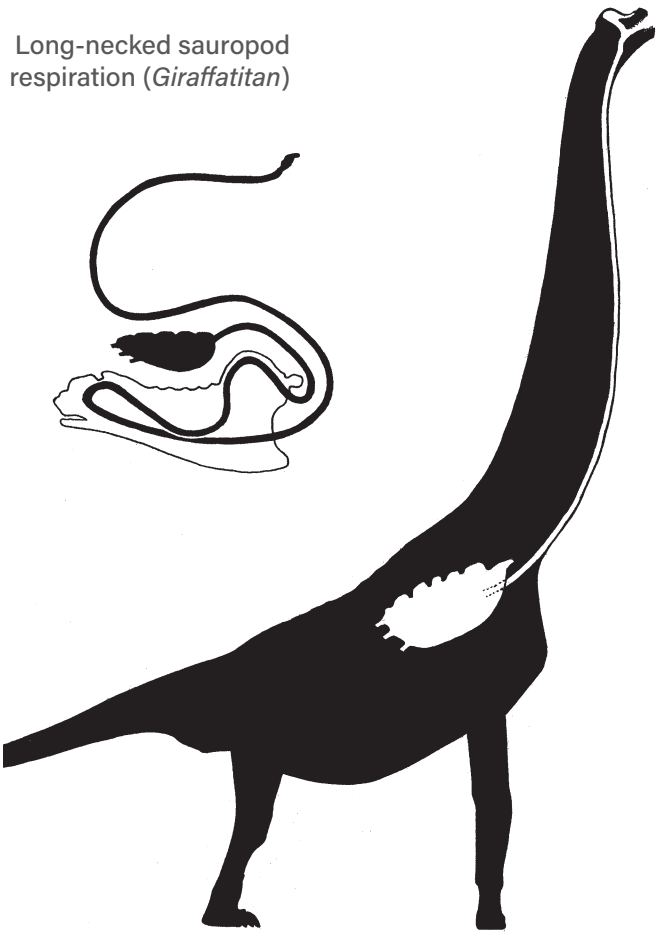
The system is set up in such a manner that most of the fresh inhaled air does not pass through the gas-exchange portion of the lungs but instead goes first to the air sacs, from where it is injected through the entire lungs in one direction on its way out. Because this unidirectional airflow eliminates the stale air that remains in dead-end lungs at the end of each breath and allows the blood and airflow to work in opposite, countercurrent directions that maximize gas exchange, the system is very efficient. Some birds can sustain cruising flight at levels higher than Mount Everest and equaling those of jet airliners.

Neither the first theropods nor prosauropods show clear evidence that they possessed air sacs, and aside from their lungs therefore being dead-end organs or close to it, little is known about their respiration. In the first avepod theropods some of the vertebrae were pneumatic, indicating the presence of air sacs. Also, the hinge jointing of the ribs increased, indicating that they were probably helping to ventilate the lungs by inflating and deflating trunk air sacs. As theropods evolved, the hinge jointing of the ribs further increased, as did the invasion of the vertebrae by air sacs until it reached the hips. Also, the chest ribs began to shorten, probably because the lungs, set up into a corrugated ceiling of ribs, were becoming smaller and stiffer as the air sacs did more of the work. By this stage the air-sac complex was probably approaching the avian condition, and airflow in the lungs should have been largely unidirectional. The sternum was still small, but the gastralia may have been used to help ventilate the ventral, belly air sacs.

Alternatively the air sacs were limited to the rib cage as they are in some flightless birds—the extra-long belly ribs of birds with big abdominal air sacs are absent in theropods. In many aveairfoilan theropods the ossified sternum was as large as it is in ratites and juvenile birds and was attached to the ribs via ossified sternal ribs, so the sternal plate was combining with the gastralia to inflate and deflate the air sacs. Also, ossified uncinate processes are often present, indicating that the bellows-like action of the rib cage was also improved. At this stage the respiratory complex was probably about as well developed as it is in some modern birds.

The very few researchers who think birds are not dinosaurs deny that theropods breathed like birds. Some propose that theropod dinosaurs had a crocodilian liver-pump system. Aside from theropods not being close relatives of crocodilians, they lacked the anatomical specializations that make the liver-pump system possible—a smooth rib cage ceiling, a lumbar region, and a mobile pubis. Instead, some of the theropods' adaptations for the avian air-sac system—the corrugated rib cage ceiling created by the hinged rib articulations, the elongated belly ribs—would have prevented the presence of a mobile liver. Proponents of the avepod liver pump point to the alleged presence of a deep liver within the skeletons of some small theropods. The fossil evidence for these large livers is questionable, and in any case, predators tend to have big livers, as do some birds. The existence of a crocodilian liver-pump lung ventilation system in dinosaurs can be ruled out.

Long-necked sauropod respiration (*Giraffatitan*)



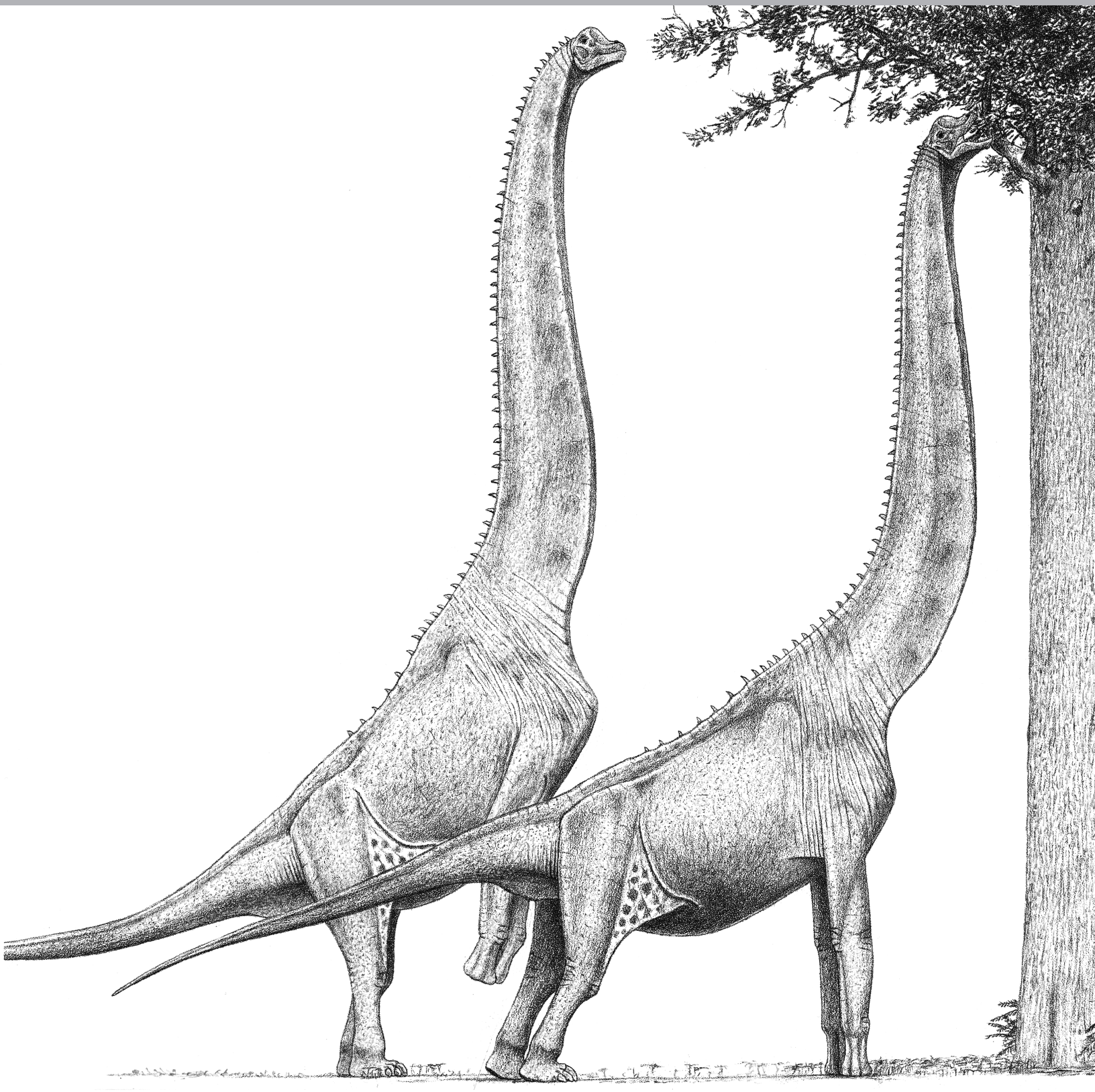
Sauropods show strong evidence that they, too, independently evolved a complex air-sac system. The vertebrae were usually highly pneumatic. Also, all the ribs were hinge jointed, even the belly ribs, which one would expect to instead be solidly anchored in order to better support the big belly. A corrugated rib cage ceiling favors rigid lungs. Most researchers agree that the air sac–filled vertebrae and mobile belly ribs of sauropods are strong signs that they had an air sac–driven respiratory complex that probably involved unidirectional airflow and approached, but did not fully match, the sophistication and efficiency of those of birds. Because sauropods lacked gastralia, the air sacs should have been limited to the rib cage. Sauropods pose an interesting respiratory problem because most of them had to breathe through very long tracheae, which created a large respiratory dead space that had to be overcome with each breath. This is paralleled in long-necked birds such as swans, which have a looped trachea in their chest, so an extra-long trachea does not critically inhibit breathing. Presumably the great air capacity of the air sacs helped sauropods completely flush the lungs with fresh air during each breath.

Mammal red blood cells lack a nucleus, which increases their gas-carrying capability. The red blood cells of reptiles, crocodilians, and birds retain a nucleus, so those of dinosaurs should have as well.

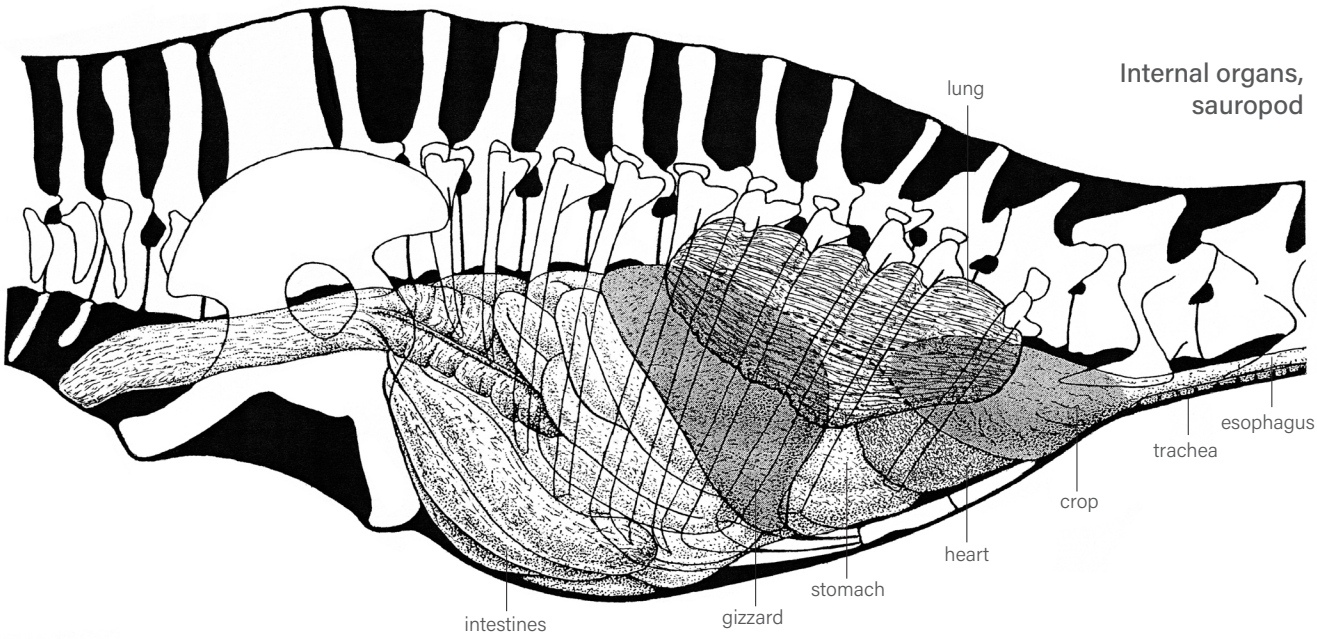
DIGESTIVE TRACTS

In a number of dinosaur fossils from a number of groups, gastroliths, or gizzard stones, are preserved within the rib cage, often as bundles of stones. In some dinosaur formations large numbers of polished stones are present even though geological forces that could explain their presence are absent. This evidence indicates that many dinosaurs, herbivores especially, utilized stone-rolling gizzards. But not all; a number of articulated skeletons show no sign of their presence, and they have not yet been found in blade-toothed predatory dinosaurs.

The digestive tracts of predatory theropods were relatively short, simple systems that quickly processed the easily digested chunks of flesh bolted down by the simple scissoring action of the serrated teeth. Coprolites attributable to large theropods often contain large amounts of undigested bone, confirming the rapid passage of food through the tract. A few preserved remains indicate that nonvolant predatory dinosaurs retained a somewhat larger digestive tract than do birds with their overall lighter complexes, starting with a large crop. Some vegetarian theropods used numerous gastroliths in a crop to break up plant material. Like herbivorous birds, most sauropods lacked the ability to chew the plant materials they ingested. The fodder was physically broken down in the gizzard, which often contained stones. Because these are not found in



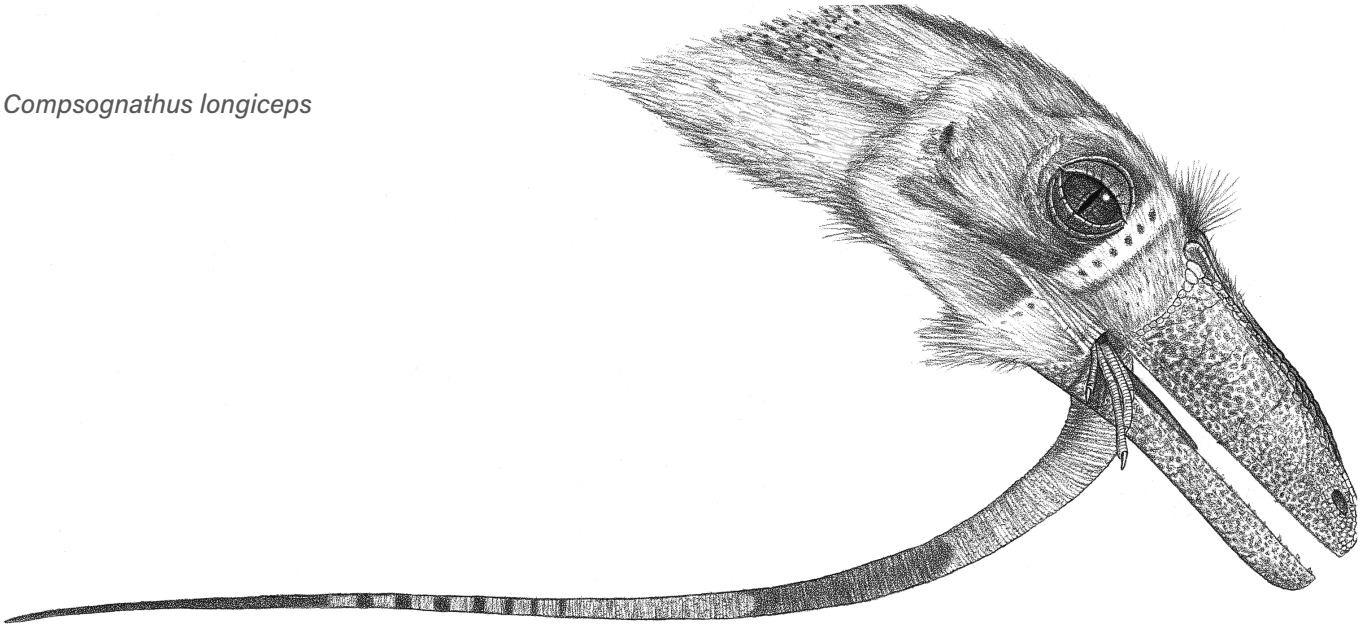
Giraffatitan brancai



large numbers, these sauropods may have used the stones not so much to directly pulp and grind plant material as to stir it up. Sauropods had large rib cages that contained the long, complex digestive tracts needed to ferment and chemically break down leaves and twigs. The system was taken to an extreme in the broad-bellied titanosaurs.

The cheeks that appear to have been present on at least some prosauropods, early sauropods, and therizinosaurs should have allowed them to mash food before swallowing. Food chewing may explain why prosauropods did not have particularly big, fermenting tummies. But it was the ornithischians that fully exploited the cheek-dependent system. After cropping food with their beaks, they could break up plant parts with their dental batteries. As some of the food fell outside the tooth rows, it was held in the elastic cheek pouches until the tongue swept it up for further processing or swallowing. Having taken the evolution of dinosaur dental complexes the furthest, hadrosauriformes had modest-sized abdomens to further process the well-chewed fodder. At the other end of this factor, some ornithischians had relatively weakly developed tooth complexes and used massive digestive tracts contained in enormous bellies to ferment and break down food. In pachycephalosaurs the digestive tract was further expanded by broadening the base of the tail in order to accommodate an enlargement of the intestines behind the pelvis. A few ornithischians supplemented plant processing with dense, food-grinding bundles of gastroliths. In herbivores the ingested fodder,

Compsognathus longiceps



bacterial gut flora, feces, and gizzard stones if present make up 10 to 20 percent of the animal's total mass.

There is no evidence that any dinosaur evolved a highly efficient ruminant-like system in which herbivores chew their own cuds. Such a system works only in animals of medium size in any case, and it was not suitable for the most titanic dinosaurs.

SENSES

The large eyes and well-developed optical lobes characteristic of most dinosaurs indicate that vision was usually their primary sensory system, as it is in all birds. Reptiles and birds have full color vision extending into the ultraviolet range, so dinosaurs very probably did too. The comparatively poorly developed color vision of most mammals is a heritage of the nocturnal habits of early mammals, which reduced vision in the group to such a degree that eyesight is often not the most important of the senses. Our own skew toward color vision is different from that typical of animals, being more oriented to green. Reptile eyesight is about as good as that of well-sighted mammals, and birds tend to have very high-resolution vision, both because their eyes tend to be larger than those of reptiles and mammals of similar body size and because they have higher densities of light-detecting cones and rods than mammals. The cones and rods are also spread at a high density over a larger area of the retina than in mammals, in which high-density light cells are more concentrated at the fovea (so our sharp field of vision covers just a few degrees). Some birds have a secondary fovea. Day-loving raptors can see about three times better than people, and their sharp field of vision is much more extensive, so birds do not have to point their eye at an object as precisely as mammals to focus on it. Birds can also focus over larger ranges, 20 diopters compared to 13 diopters in young adult humans. The vision of the bigger-eyed dinosaurs may have rivaled this level of performance. The dinosaurs' big eyes have been cited as evidence for both daylight and nighttime habits. Large eyes are compatible with either lifestyle—it is the (in this case unknowable) structure of the retina and pupil that determines the type of light sensitivity.

Birds' eyes are so large relative to the head that they are nearly or entirely fixed in the skull, so looking at specific items requires turning the entire head. The same was likely to have been true of smaller-headed dinosaurs. Dinosaurs with larger heads should have had more mobile eyeballs that could scan for objects without rotating the entire cranium. The eyes of most dinosaurs faced to the sides, maximizing the area of visual coverage at the expense of the binocular view directly ahead. Some birds and mammals—primates most of all—have forward-facing eyes with overlapping fields of vision, and in at least some cases vision includes a binocular, stereo effect that provides depth perception. Tyrannosaurid, ornithomimid, and many aveairfoilan theropods had partly forward-facing eyes with overlapping vision fields. Whether vision was truly stereo in any or all of these dinosaurs is not certain; it is possible that the forward-facing eyes were an incidental but perhaps beneficial side effect of the expansion of the back of the skull to accommodate larger jaw muscles in tyrannosaurids, *Tyrannosaurus* most of all.

Most birds have a poorly developed sense of smell, the result of the lack of utility of this sense for flying animals, as well the lack of space in heads whose snouts have been reduced to save weight. Exceptions are some vultures, which use smell to detect rotting carcasses hidden by deep vegetation, and grub-hunting kiwis. As nonfliers with large snouts, many reptiles and mammals have very well-developed olfaction, sometimes to the degree that it is a primary sensory system, canids being a well-known example. Dinosaurs often had extremely well-developed, voluminous nasal passages, with abundant room at the back for large areas of olfactory tissues. In many dinosaur brains the olfactory lobes were large, verifying their effective sense of smell. Herbivorous dinosaurs probably had to be approached from downwind to avoid their sensing and fleeing from an attack, and it is possible that olfaction was as important as vision in the smaller-eyed ankylosaurs. Among theropods the tyrannosaurs and dromaeosaurs had especially excellent olfaction, useful for finding both live prey and dead carcasses.

Mammals have exceptional hearing, in part because of the presence of large, often movable outer ear pinnae that help catch and direct sounds into the ear opening, and especially because of the intricate middle ear made up of three elements that evolved from what were once jaw bones. In some mammals hearing is the most important sense, bats and cetaceans being the premier examples. Reptiles and birds lack fleshy outer ears, and there is only one inner ear bone. The combination of outer and complex inner ears means that mammals can pick up sounds at low volume. Birds partly compensate by having more auditory sensory cells per unit length of the cochlea, so sharpness of hearing and discrimination of frequencies are broadly similar in birds and mammals. Where mammalian hearing is markedly superior is in high-frequency sound detection. In many reptiles and birds the auditory range is just 1–5 kHz; owls are exceptional in being able to pick up from 250 Hz to 12 kHz, and geckos go as high as 10 kHz. In comparison, humans can hear 20 kHz, dogs up to 60 kHz, and bats 100 kHz. At the other end of the sound spectrum, some birds can detect very low frequencies: 25 Hz in cassowaries, which use this ability to communicate over long distances, and just 2 Hz in pigeons, which may detect approaching storms. It has been suggested that cassowaries use their big, pneumatic head crests to detect low-frequency sounds, but pigeons register even basser sounds without a large organ.

In the absence of fleshy outer and complex inner ears, dinosaur hearing was in the reptilian-avian class, and they could not detect very high frequencies. Nor were the auditory lobes of dinosaur brains especially enlarged, although they were not poorly developed either. Nocturnal, flying, rodent-hunting owls are the only birds that can hear fairly

high-frequency sounds, so certainly most and possibly all dinosaurs could not hear them either. Oviraptorosaurs had hollow head crests similar to those of cassowaries, hinting at similar low-frequency sound detection abilities. The big ears of large dinosaurs had the potential to capture very low frequencies, allowing them to communicate over long distances. It is unlikely that hearing was the most important sense in any dinosaur, but it was probably important for detection of prey and predators, and for communication, in all species.

VOCALIZATION

No living reptile has truly sophisticated vocal abilities, which are best developed in crocodilians. Some mammals do, humans most of all. A number of birds have limited vocal performance, but many have evolved a varied and often very sophisticated vocal repertoire not seen among other vertebrates outside of people. Songbirds sing, and a number of birds are excellent mimics, to the point that some can imitate artificial sounds such as bells and sirens, and parrots can produce understandable humanlike speech. Some birds, swans particularly, possess elongated tracheal loops in the chest that they use to produce high-volume vocalizations. Cassowaries call one another over long ranges with very low-frequency sounds, and so do elephants. Birds possess the intricate voice boxes needed to generate complex vocalizations. Among dinosaur fossils only an ankylosaur skull includes a complete voice box. The complicated structure of the armored dinosaurs' larynx suggests vocal performance at an avian level, perhaps high-end performance, and such may have been true of other dinosaurs. The long trachea of long-necked dinosaurs should have been able to generate powerful low-frequency sounds that could be broadcast over long ranges. Vocalization is done through the open mouth rather than through the nasal passages, so complex nasal passages acted as supplementary resonating chambers. This system was taken to an extreme in the large-crested lambeosaurine hadrosaurs with their convoluted nasal tracts. It is doubtful that any nonavian dinosaur had vocal abilities to match the more sophisticated examples seen in the most vocally sophisticated birds and mammals. Although we will never know what dinosaurs sounded like, and the grand roars of dinosaur movies are not likely, there is little doubt that the Mesozoic forests, prairies, and deserts were filled with their voices.

GENETICS

As more fossils are found in different levels of geological formations, the evidence is growing that dinosaurs enjoyed high rates of speciation that boosted their diversity at any given time. And over time, via a rapid turnover of species, most did not last for more than a few hundred thousand years before being replaced by new species one way or another. The same is true of birds, which have more chromosomes than slower-evolving mammals. Dinosaurs presumably had the same genetic diversity as their direct avian descendants, which may have been a driving force behind their multiplicity.

DISEASES AND PATHOLOGIES

Planet Earth was infested with a toxic soup of diseases and other dangers that put all dinosaurs at high risk. The disease problem was accentuated by the global greenhouse effect, which maximized the tropical conditions that favored disease organisms, especially bacteria and parasites. Biting insects able to spread assorted diseases were abundant during the Mesozoic; fossils have been found in amber and fine-grained sediments. Reptile and bird immune systems operate somewhat differently from those of mammals; in birds the lymphatic system is particularly important. Presumably the same was true of their dinosaur ancestors.

Dinosaur skeletons often preserve numerous pathologies. Some appear to record internal diseases and disorders. Fused vertebrae are fairly common. Also found are growths that represent benign conditions or cancers. Most pathologies are injuries caused by stress or wounds; the latter often became infected, creating long-term, pus-producing lesions that affected the structure of the bone. Injuries tell us a lot about the activities of dinosaurs. Some dinosaur skeletons are so afflicted with serious defects that one of them very probably killed the beast, especially if it was immature.

The predaceous theropods are, not surprisingly, especially prone to show signs of combat-related injury. One *Allosaurus* individual shows evidence of damage to its ribs, tail, shoulder, feet, and toes as well as chronic infections of a foot, finger, and rib. The tail injury, probably caused by a kick or fall, occurred early in life. Some of the injuries, including those to the feet and ribs, look severe enough that they may have limited its activities and contributed to its death. A wound in another *Allosaurus* tail appears to have been inflicted by the spike of a stegosaur. The famous *Tyrannosaurus* "Sue" had problems with its face and tail as well as a neck rib, finger, and fibula. The head and neck wounds appear to have been caused by other *Tyrannosaurus* and in one case had undergone considerable healing. The sickle claw–bearing toes of dromaeosaurs and troodonts frequently show signs of stress damage.

Among herbivorous dinosaurs, stegosaur tail spikes are often damaged or even broken and then healed, verification that they were used for combat. The horn of a *Triceratops* was bitten off by a *Tyrannosaurus*, according to the tooth marks, and then healed during the following years, indicating that the prey survived face-to-face combat with the great predator. Whether the predator survived the combat is unknown. Healed bite marks in the tails of sauropods and duck-billed hadrosaurs indicate that they too survived attacks by allosaurs and tyrannosaurs, respectively. Sauropods, despite or perhaps because of their size and slow speeds, show relatively little evidence of injury.

Parkosaurus and troodont

BEHAVIOR

BRAINS, NERVES, AND INTELLIGENCE

Assessing brain power is complicated because many factors are involved. One that has long been used is the mass of the brain relative to total body mass at a given size. Within the context that brains of a given performance level tend to become smaller relative to the body as size increases—elephant brains are many times absolutely larger than those of people while being many times smaller relative to body weight, and we are overall more intelligent—relatively bigger brains are likely to produce higher cognition. Also important is brain structure, with birds and mammals having more complex schemes including large forebrains. Adding to the complications is the neural density factor. Reptiles have much lower neural density relative to brain mass than mammals and birds, and the latter are markedly higher in this regard than mammals. The last point helps explain why birds with absolutely small brains such as crows and parrots achieve levels of thinking comparable to those of some far larger-headed primates. Avian brains are also markedly more energy efficient, their neurons requiring less glucose to process information. Big brains packed with lots of neurons can correlate with metabolism in that low-energy animals cannot produce enough metabolic power to operate high-cognition brains, which require a high metabolism. Less clear is whether energetic animals automatically have similarly energetic brains. In particular, it is not known whether reptilian brains can have high neural densities even if the animals run at high metabolic rates.

The brains of the great majority of dinosaurs were reptilian both in size relative to the body and in structure. There was some variation in size compared to body mass: the giant tyrannosaurids had unusually large brains for dinosaurs of their size, and so did the duck-billed hadrosaurs they hunted. However, even the diminutive brains of sauropods and stegosaurs were within the reptilian norm for animals of their great mass.

Taken at face value, the small, fairly simple brains common to most dinosaurs seem to indicate that their behavioral repertoire was limited compared to those of birds and mammals, being more genetically programmed and stereotypical. But if dinosaurs are presumed to have been stable-temperature endotherms via high metabolic rates, then it is possible, albeit by no means certain, that their neural densities were in the mammalian or, since dinosaurs include birds, even in the avian range. This has led to estimates that bigger-brained dinosaurs such as tyrannosaurs were as smart as the cleverest birds, as well as primates other than humans, and may have used simple, crafted nonstone/nonmetal tools. "Crafting" implies modifying an object in some manner to make it usable, rather than just picking up a rock and using it to smash open a hard-shelled item. Crafting can be as simple as stripping leaves and side branches off a twig to make it into a probe or lever. But this is by no means certain when it comes to the majority of dinosaurs, whose thinking organs were reptilian in form. That such energetic dinosaurs had the low neural densities of reptiles unable to sustain high levels of activity appears unlikely, but their simple brains may have precluded the neural concentrations of birds. It is therefore not possible to reliably assess the intelligence of dinosaurs with reptilian-form brains at this time, and it may never be doable. Even if big theropods were not supersmart, it is pertinent that even small-brained animals can achieve remarkable levels of mental ability. Fish and lizards can retain new information and learn new tasks. Many fish live in organized groups. Crocodilians care for their nests and young. Social insects with tiny neural systems live in organized colonies that rear the young, enslave other insects, and even build large, complex architectural structures. It is not unthinkable that dinosaurs up to the biggest sauropods could use sticks and leafy branches to scratch themselves if they could reach close enough to their bodies with their mouths, use heavy sticks to knock down otherwise unreachable choice food items, or build leafy branch piles over water holes to protect them when not in use, as elephants do.

The major exception to dinosaurian reptile brains appeared in the birdlike aveairfoilan theropods. Their brains were proportionally larger, falling into the lower avian zone, as did their complexity. It is possible if not probable that neural densities were approaching if not at the avian level. It may be that the expanded and upgraded brains of aveairfoilans evolved at least in part in the context of the initial stages of dinosaurian flight. Presumably the bigger-brained dinosaurs were capable of more sophisticated behavior than other dinosaurs. Use of very simple tools is plausible, all the more so because many small nonavian avepods that had supple-fingered hands may have been able to manipulate devices, in addition to using their mouths in ways similar to tool-using birds. On the other hand, use of crafted tools in wild birds is not extensive, and it may well be that no Mesozoic dinosaur did this. If any did, tool utilization may have occurred in the context of prying open hard-shelled food items, or probing insect holes in search of prey. The insectivorous alvarezsaurs might have been especially prone to the latter, but their stout and powerful arms and hands were much better suited for bursting open insect colonies than holding tools.

The enlarged spinal cavity in the pelvic region of many small-brained dinosaurs was an adaptation to better coordinate the function of the hind limbs and is paralleled in big ground birds. The great length of some dinosaurs posed a potential problem in terms of the time it took for electrochemical impulses to travel along the nerves. In the biggest sauropods, a command to the end of the tail and the response back could have had to travel as much as 75 m (250 ft) or more. Synaptic gaps where chemical reactions transmit information slow down the impulses, so this problem could have been minimized by growing individual nerve cords as long as possible.

SOCIAL ACTIVITIES

Land reptiles do not form organized groups. Birds and mammals often do, but many do not. Most big cats, for instance, are solitary, but lions are highly social. Some, but not all, deer form herds.

That dinosaurs often formed social groups is supported by some single-species bone beds that do not appear to have been death traps that slowly accrued fossils over time, or perhaps resulted from droughts that compelled numerous individuals to gather at a water source where they starved to death as the vegetation ran out. Some accumulations appear to have been the result of sudden events caused by volcanic ashfalls, flash floods, drownings when many dinosaurs crossed fast-flowing streams, or dune slides. Such bone beds, which in some cases suggest the existence of very large herds, usually consist of herbivorous dinosaurs.

The presence of a number of individuals of a single species of theropod in association with the skeleton of a potential prey animal has been cited as evidence that predatory dinosaurs sometimes killed and fed in packs. It is, however, often difficult to explain why so many theropods happened to die at the same time while feeding on a harmless carcass. It is more probable that the theropod skeletons represent individuals killed by other theropods in disputes over feeding privileges, an event that often occurs when large carnivorous reptiles and mammals compete over a kill.

Trackways are the closest thing we have to motion pictures of the behavior of fossil animals. A significant portion of the trackways of a diverse assortment of dinosaurs are

Trackways of a herd of sauropods

solitary, indicating that the maker was not part of a larger group. It is also very common for multiple trackways of a variety of dinosaur species to lie close together on parallel paths. In some cases this may be because the track makers were forced to follow the same path along a shoreline even if they were moving independently of one another. But many times the parallel trackways are crisscrossed by the trackways of other dinosaurs that appear to have been free to travel in other directions. The large number of parallel trackways is therefore evidence that many species of predatory and herbivorous dinosaurs of all sizes often formed collectives that moved as pods, flocks, packs, and herds.

The degree of organizational sophistication of herbivorous dinosaur groups was likely variable. That of the big dinosaurs was probably similar to that in fish schools and less developed than that in organized mammal herds. Suggestions that the trackways of sauropods show that the juveniles were ringed by protective parents have not been borne out, and it is unlikely that very large dinosaurs directly cared for and protected offspring that were so tiny when they came out of their eggs or nests. Trackways never show very large adults and their very small offspring moving together, which makes sense because the former would have accidentally stomped on the latter, which would not have been able to keep up with their parents. When adult plant eaters were less enormous, perhaps a half tonne or less, then having their juveniles alongside would have been practical, as with ratites and their chicks. Flocking birds almost always fly in single-species groups. On open ground where a lot of species dwell, herbivores such as wildebeest, zebras, ostriches, elephants, and gazelles often form collective herds, each taxon bringing its own best predator-detection system into the mix. One can imagine hadrosaurs, ornithomimids, and ornithopods of assorted sizes doing the same, but multispecies bone beds indicating that dinosaurs did this have yet to be uncovered, so perhaps they did not. Nor is it likely that theropod packs employed tactics as advanced as those attributed to canid packs or lion prides.

REPRODUCTION

It has been suggested that some dinosaur species exhibit robust and gracile morphs that represent the two sexes. It is difficult to either confirm or deny many of these claims because it is possible that the two forms represent different species. Males are often more robust than females, but there are exceptions. Female raptors are usually larger than the males, for instance, and the same is true of some whales. Attempts to use the depth of the chevron bones beneath the base of the tail to distinguish males from females have failed because the two factors are not consistent in modern reptiles. Heterodontosaurs appear to come both with small tusks and without, and the former may be the males. Head-crested oviraptorosaurs and dome-headed pachycephalosaurs may be males if they are not mature individuals of both sexes. On the other hand, among cassowaries it is the females that have somewhat larger crests. This is atypical for crested birds, in which males have markedly larger display structures. The robust form of *Tyrannosaurus* has been tentatively identified as the female based on the inner bone tissues associated with egg production in birds, but the distribution of the stout and gracile morphs of this genus over stratigraphic time is more

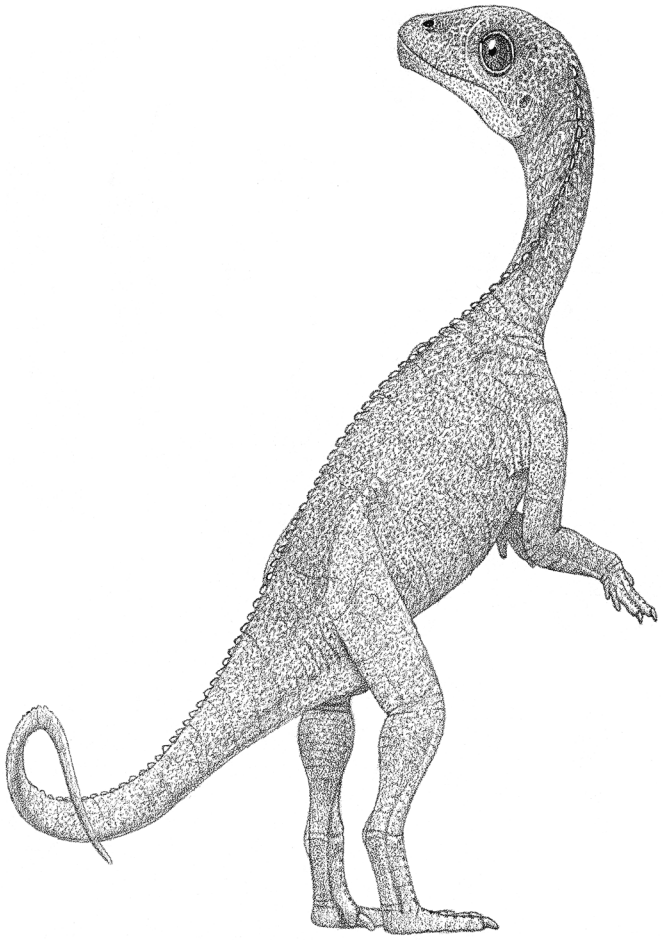
Hypacrosaurus stebingeri nest

compatible with different species than with sexes. What is more suggestive of boys and girls is variation in size of the orbital bosses of *Tyrannosaurus* at a given geological level, although ontogeny may also be a factor. While preparing this book, I realized that a pair of fairly complete *Allosaurus* skulls from the same quarry share features indicating they are a distinct species, yet they come in a deep and a shallow overall shape, providing perhaps the best evidence of dinosaurian gender identity yet observed.

Reptiles and some birds and mammals including humans achieve sexual maturity before reaching adult size, but most mammals and extant birds do not. Females that are producing eggs deposit special calcium-rich tissues on the inner surface of their hollow bones. The presence of this tissue has been used to show that a number of dinosaurs began to reproduce while still immature in terms of growth. The presence of still-growing dinosaurs brooding their nests confirms this pattern. Most dinosaurs probably became reproductive before maturing. Exceptions may have been ceratopsids and hadrosaurs, whose display organs did not become completely developed until they approached adult proportions.

The marvelous array of head and body crests, frills, horns, hornlets, spikes, spines, tail clubs, bristles, and feathers evolved by assorted dinosaurs shows that many were under strong sexual selective pressure to develop distinctive display organs and weapons to identify themselves to other members of their species, and to succeed in sexual competition. The organs we find preserved record only a portion of these visual devices—those consisting of soft tissues and color patterns are largely lost. How these organs were used varied widely. Females used display organs to signal males of the species that they were suitable and fertile mates. Males used them both to intimidate male rivals and to attract and inseminate females.

Healthy animals in their reproductive prime are generally able to dedicate more resources to growing superior-quality displays that are better able to attract mates in similarly fine condition. Use of display organs in sexual attraction and competition can be a relatively peaceful affair, and this system was taken to its dinosaurian height among the hadrosaurs with their spectacular head crests. Many dinosaurs probably engaged in intricate ritual display movements and vocalizations during competition and courtship that have been lost to time. The head and body display surfaces of many dinosaurs were oriented to the sides, so they had to turn themselves to best flaunt their display. The ceratopsians, whose head frills were most prominent in front view with the frill tilted up, were a major exception. The domes adorning pachycephalosaur heads were at least as prominent in front as in side view and may also have been tilted forward to intimidate opponents. Among the predatory avepods, the transverse head crest of *Cryolophosaurus* and the horns and domes of some abelisaurs provided unusual frontal displays. The same was true of the crest of the rather small-headed brachylophosaur hadrosaurs.



Mussaurus patagonicus hatchling

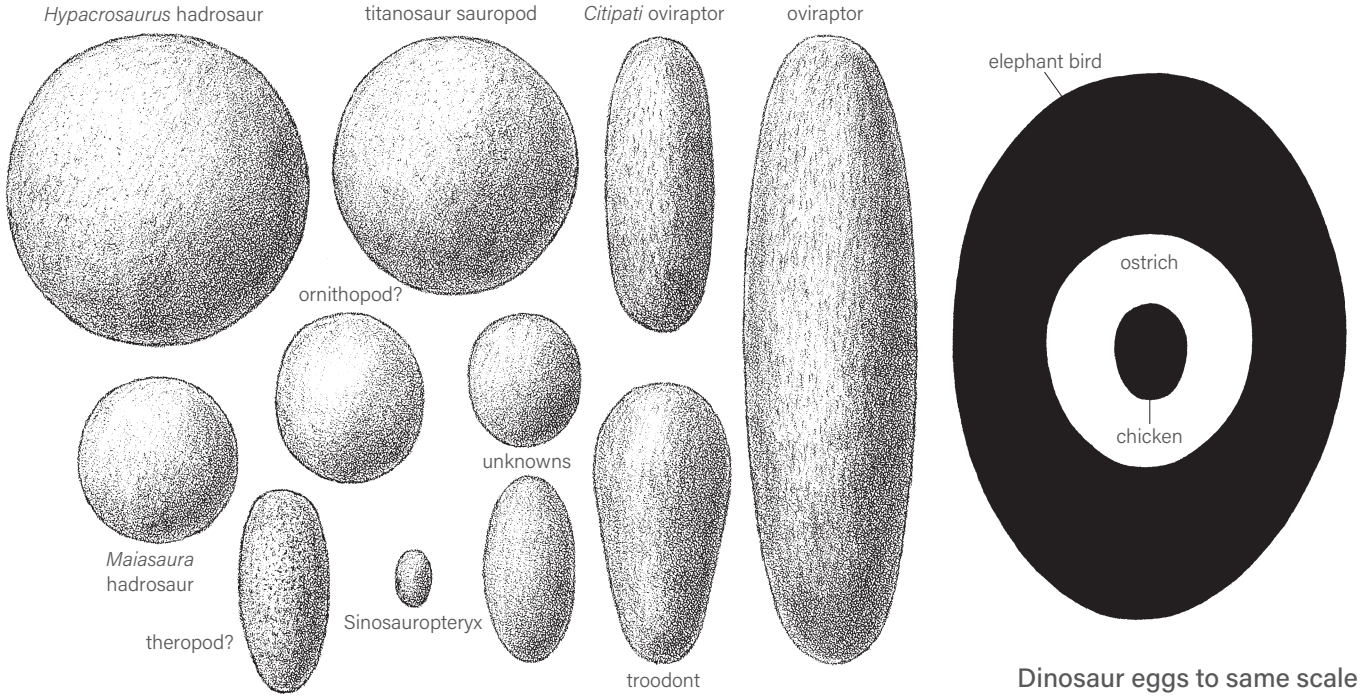
Intraspecific competition is often forceful and even violent in animals that bear weapons. Sauropods could have reared up and assaulted one another with their thumb claws. The iguanodonts' thumb spikes were potentially even more dangerous intraspecific weapons. Domeheads may have battered each other's broad flanks with their heads. Whether they used their rounded domes to headbutt like bighorn sheep is controversial. Male ankylosaurids are quite likely to have pummeled one another with their tail clubs, and other ankylosaurs probably locked their shoulder spines and engaged in strength-testing shoving matches. Multihorned ceratopsids may have interlocked their horns and done the same. Healed wounds indicate that ceratopsids also used their horns to injure one another. Tusked male heterodontosaurs may have done the same thing. The conceit that males have evolved means to avoid lethally injuring one another in reproductive contests is true in many cases, but not in others. Male hippos and lions suffer high mortality from members of their own species, and the same may have been true of theropods, ceratopsians, and big-thumb-spiked iguanodonts.

In reptiles and birds, the penis or paired penises (if either are present) and the testes are internal, and this was

the condition in dinosaurs. Most birds lack a penis, but whether any dinosaur shared this characteristic is unknown. Presumably copulation was a quick process that occurred with the female lowering her shoulders and swinging her tail aside to provide clearance for the male, which reared behind her on two legs or even one leg while placing his hands on her back to steady them. The need of sauropods to copulate supports the ability of these giants, including the biggest and those with long forelimbs, to stand on the hind legs alone. The vertical armor plates of stegosaurs probably required a modification, with the male resting his hands on one side of the female's pelvis.

At least some dinosaurs from theropods to sauropods to ornithopods produced hard-shelled eggs like those of birds, rather than the softer-shelled eggs of reptiles including crocodilians, and mammals. The evolution of calcified shells may have precluded live birth, which is fairly common among reptiles and is absent in birds. On the other hand, eggs of prosauropods and protoceratopsids appear to have been soft shelled, indicating that there was considerable variation in the feature in dinosaurs, perhaps even within subgroups. If so, that could help explain why remains of dinosaur eggs are surprisingly scarce through much of the Mesozoic. For example, not a single eggshell fragment attributable to the many sauropod species that inhabited the enormous Morrison Formation has yet been found. A fast-growing and diverse collection of eggs and nests is now known for a wide variety of Jurassic and Cretaceous dinosaurs, most from the latter half of the latter period. Firmly identifying the producer of a given type of egg requires the presence of intact eggs within the articulated trunk skeleton, or identifiable embryo skeletons within the eggs, as well as adults found atop their nests in brooding posture. Because each dinosaur group produced distinctive types of eggshells and shapes, the differences can be used to further identify their origin, although the producers of many types remain obscure. Dinosaur eggs ranged from near-perfect spheres to highly elongated and in some cases strongly tapered. The surface texture of the egg was crenulated in some, and bumpy in others. The arrangement of eggs within dinosaur bodies and in their nests shows that they were formed and deposited in pairs as in reptiles, rather than singly as in birds. Even small reptiles lay small eggs relative to the size of the parent's body, whereas birds lay proportionally larger eggs. The eggs of small dinosaurs are intermediate in size between those of reptiles and birds. It is interesting that no known Mesozoic dinosaur egg matches the size of the gigantic 12 kg (25 lb) eggs laid by the flightless elephant bird *Aepyornis*, which, as big as it was at nearly 400 kg (800 lb), was dwarfed by many dinosaurs. The eggs of the huge sauropods, for instance, weighed less than 1 kg (2 lb). The largest dinosaur eggs discovered so far weighed 5 kg (11 lb) and probably belonged to 1-tonne-plus oviraptors.

There are two basic reproductive stratagems, r-strategy and K-strategy. K-strategists are slow breeders that produce few young; r-strategists produce large numbers of offspring that offset high losses of juveniles. Rapid reproduction has an advantage. Producing large numbers of young allows a species to quickly expand its population when conditions are suitable, so r-strategists are "weed species" able to rapidly colonize new territories or promptly recover their population after it has crashed for one reason or another. As far as we know, Mesozoic dinosaurs were consistently r-strategists that typically laid large numbers of eggs in the breeding season, although dinosaurs isolated



Dinosaur eggs to same scale

Oviraptor *Citipati* incubating a nest, based on a fossil, with feathers drawn short enough to show eggs

on predator-free islands might have been slow breeders. This may explain why dinosaurs laid smaller eggs than birds, most of which produce a modest number of eggs and provide the chicks with considerable parental attention. One r-strategist bird group is the big modern ratites, which produce numerous eggs. This is in contrast to the big island ratites that laid only one to a few oversized eggs a year because the young were not at risk of being snarfed up by predators, until humans liquidated the populations in part by eating the giant eggs. Sauropods appear to have placed the largest number of eggs in a single nest, up to a few dozen. Giant dinosaurs were very different in this respect from giant mammals, which are K-strategists that produce few calves that then receive extensive care over a span of years. Nor did any dinosaur nurse its young via milk-producing mammary glands. It is possible that some dinosaurs produced a "milk"-like substance in the digestive tract that was regurgitated to their young, as pigeons do, but there is no direct evidence of this.

It was long tacitly assumed that, like most reptiles, dinosaurs paid little or no attention to their eggs after burying them. A few lizards do stay with the nest, and pythons actually incubate their eggs with muscle heat. Crocodilians often guard their nests and hatchlings. All birds lavish attention on their eggs. Nearly all incubate the eggs with body heat; the exception is megapode fowl that warm eggs in mounds that generate heat via fermenting vegetation. The fowl carefully regulate the temperature of the nest by adding and removing vegetation to and from the mound. But when megapode chicks hatch, they are so well developed that the precocial juveniles quickly take off and survive on their own. The newly hatched chicks of ratites are also precocial, but they remain under the guardianship of adults that guide them to food sources and protect them from attack. Most bird chicks are altricial: they are so poorly developed when they break out of the egg that they have to be kept warm and fed by adults.

A spate of recent discoveries has revealed that the manner in which dinosaurs deposited eggs and then dealt with them and the offspring varied widely and was both similar to and distinctive from this behavior in living tetrapods.

Some dinosaur eggs whose makers have yet to be identified were buried in a manner that implies they were immediately abandoned. This was probably true of the eggs of

sauropods. The large, vegetation-covered nests that can be attributed to the giants were structured in a rather irregular manner that differs from the more organized nests tended by adults. There is evidence that at least some sauropods deposited their eggs near geothermal heat sources. Because large numbers of nests were created at the same time and place, the adult sauropods would have risked denuding the local vegetation as well as trampling their own eggs if they remained to guard their nests. Also in danger of being trampled were the hatchlings, which were thousands of times less massive than their parents. Laying so many eggs in so many nests helped overwhelm the ability of the local predators to find and eat all the eggs and emerging hatchlings, although a fossil shows a large snake feeding on a just-emerged hatchling. Some prehatchling reptiles in mass nests start vocalizing to better coordinate their synchronous emergence, even though doing so risks attracting egg and hatchling eaters. Trackways indicate that small juvenile sauropods formed their own pods, independent of multitonne adults. Other trackways further indicate that sauropod calves joined full-sized adults only after a few years, when they had reached about a tonne, large enough to keep up and not be stepped on in the process. The mature sauropods probably paid the young ones no particular notice and were unlikely to have even been closely related to them. In this scenario, the juveniles were seeking the statistical safety of being near aggressive grown-ups able to battle the biggest predators.

Also apparently forming juvenile pods were at least some ankylosaurs. The intact skeletons of over a dozen large *Pinacosaurus* juveniles have been found grouped together, apparently killed at the same moment by a dune slide. The absence of an adult suggests that the growing armored dinosaurs were moving together as an independent gang.

The compact nests of duck-billed hadrosaurs have a structural organization that suggests they were monitored by adults. Hadrosaurs may have regulated the temperatures of their mound nests like megapode fowl. The nests seem to form colonies in at least some cases, and breeding hadrosaurs were not so large that they would have stripped the local flora if they remained to care for their young. In many hadrosaur nests the eggs are so thoroughly broken up that they seem to have been trampled on over time, and skeletons of juveniles considerably larger than hatchlings have been found in the nests, so the young hadrosaurs did not immediately abandon their nests. The heads of baby hadrosaurs had the short snouts and large eyes that encourage parental behavior. These factors suggest that the parents opened the mounds as the eggs hatched and then brought food to the altricial juveniles while they remained in the nest. This arrangement would have avoided the problem of stepping on the tiny hatchlings, provided them protection from predators, and improved growth rates by supplying the nestlings with plenty of food while the youngsters saved energy by remaining immobile. What happened when hadrosaur juveniles left the nest after a few weeks or months is not certain—the still-extreme size disparity between the parents and their offspring favors the latter forming independent pods until they were large enough to join the adult herds.

Little is known about the nesting of large predatory theropods. Juvenile tyrannosaurids were unusual in having elongated snouts, the opposite of the short faces of juveniles cared for by their parents. This suggests that growing tyrannosaurids hunted independently of the adults. Suggestions that the gracile juvenile tyrannosaurids hunted prey for their parents are implausible; when food is exchanged between juveniles and adults, it is the latter who feed the former.

Because smaller dinosaurs did not face the problem of accidentally crushing their offspring, they had the potential to be more intensely parental. The best evidence for dinosaur brooding and incubating is provided by the birdlike aveairfoilan theropods, especially oviraptors. The large number of eggs, up to a few dozen in some cases, could not have been produced by a single female, so the nests were probably communal. The big ratites also nest communally. Oviraptors laid their elongated eggs in two-layered rings with an open center. Laid flat, the eggs were partly buried and partly exposed. Because eggs left open to the elements would die from exposure or predation, eggs were not left exposed unless they were intended to be protected and incubated by adults. A number of oviraptor nests have been found with an adult in classic avian brooding posture atop the eggs, the legs tucked up alongside the hips, the arms spread over the eggs. The egg-free area in the center of the ring allowed the downward-projecting pubis of the deep pelvis to rest between the eggs without crushing them; flatter-bellied birds do not need this space between their eggs. Presumably the arm and other feathers of oviraptorosaurs completely covered the eggs to protect them from inclement conditions and to retain the incubator's body heat. It is thought that brooding oviraptors were killed in place by sandstorms or more likely dune slides. The giant eggs appear to be of the type laid by oviraptors, and they too are laid in rings, in their case of enormous dimensions (up to 3 m or 10 ft across). These are the largest incubated nests known and were apparently brooded by oviraptors weighing a tonne or two—brooding by such big parents was made possible by the body being supported by the pubis between the eggs, rather than the entire body bearing down on the eggs. In troodont nests the less-elongated eggs were laid subvertically in a partial spiral ring, again with the center open to accommodate the brooder's pelvis. The size of the adult troodonts found in brooding posture atop their nests is as small as 0.5 kg (1 lb). The half-buried, half-incubated nesting habits of aveairfoilans ideally represent the near-avian arrangement expected in the dinosaurs closest to birds. We humans tend to presume that it was females that did most or all of the brooding, but in birds, including ratites, males often do a lot of the egg and nestling warming, and male cassowaries do all of it.

A problem that all embryos that develop in hard-shelled eggs face is getting out of that shell when the time is right. The effort to do so is all the harder when the egg is large and the shell correspondingly thick. Fortunately, some of the shell is absorbed and used to help build the skeleton of the growing creature. Baby birds use an "egg tooth" to achieve the breakout. The same has been found adorning the nose of titanosaur sauropod embryos, and this may have been true of other Mesozoic dinosaurs.

Whether small birdlike theropods and many other dinosaurs continued to care for their young after they hatched is not known but is plausible. The best evidence for dinosaur parenting of juveniles found so far is among small ornithischians. A compact clutch of nearly three dozen articulated juvenile (about a tenth of a kilogram, or a fifth of a pound) *Psittacosaurus* skeletons was found in intimate association with the remains of an adult over a dozen times heavier. There is dispute over whether this is a true association between a parent and its offspring; if it is, the situation seems to parallel that of some ratite birds, which gather the offspring of a number of females into a large crèche that is tended by a set of adults. It is possible that the tightly packed collection of psittacosaurs was entombed in a fossil burrow. Again, it is possible that males as well as females were at least sometimes involved to some degree in parenting, as per many living dinosaurs.

Parental care probably ranged from nonexistent to extensive in dinosaurs and in a number of cases probably exceeded that seen in reptiles or even crocodilians, rivaling that of birds. However, no dinosaur lavished its offspring with the parenting typical of mammals, and because dinosaurs did not nurse, it is likely that most of them could grow up on their own either normally, or if something happened to the grown-ups.

Ornitholestes hermanni

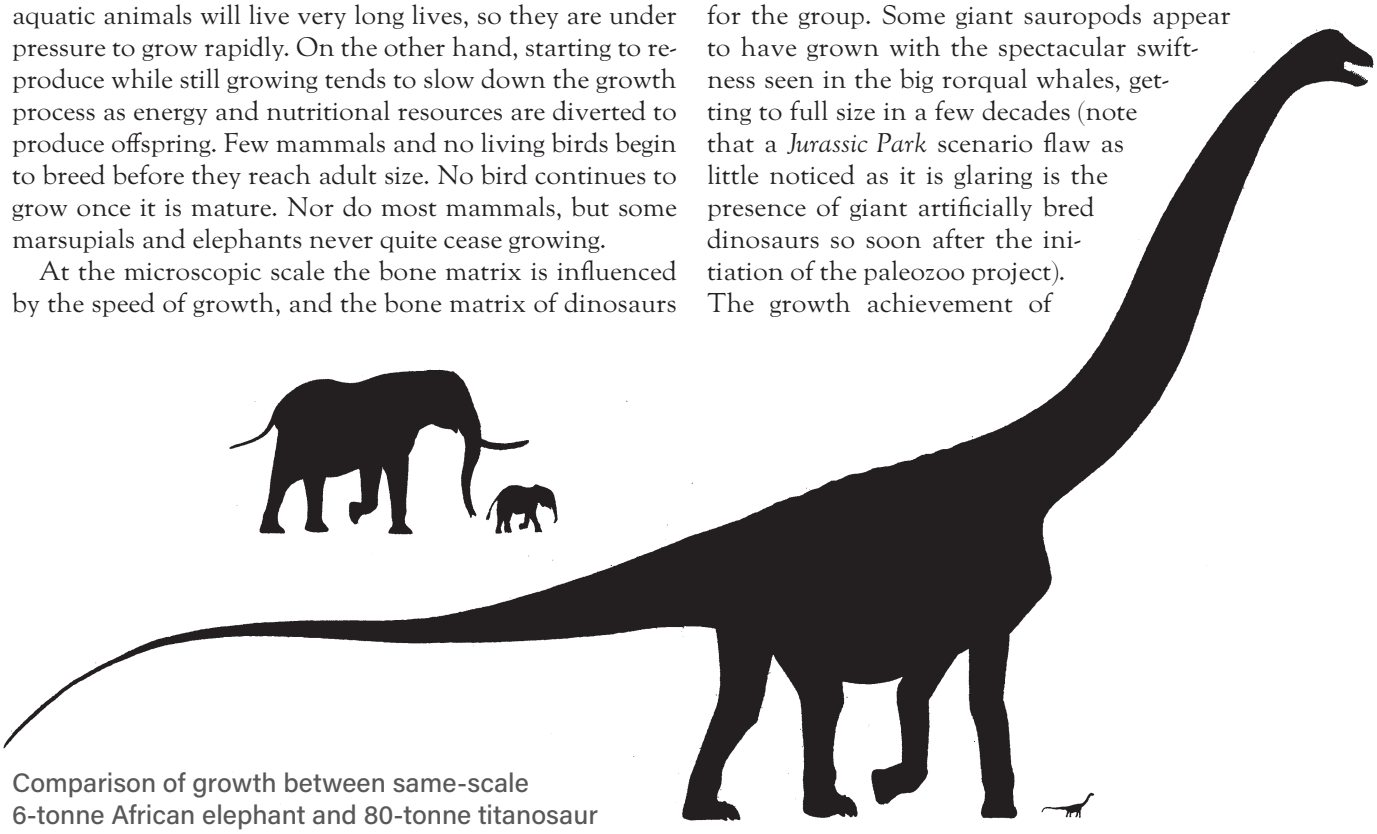
GROWTH

All land reptiles grow slowly. This is true even of giant tortoises and big, energetic (by reptilian standards) monitors. Land reptiles can grow most quickly only in perpetually hot equatorial climates, and even then they are hard pressed to reach a tonne. Aquatic reptiles can grow more rapidly, probably because the low energy cost of swimming allows them the freedom to acquire the large amounts of food needed to put on bulk. But even crocodilians, including the extinct giants, which reached nearly 10 tonnes, do not grow as fast as many land mammals. Mature reptiles tend to continue to grow slowly throughout their lives.

Some marsupials and large primates including humans grow no faster or only a little faster than the fastest-growing land reptiles. Other mammals, including other marsupials and a number of placentals, grow at a modest pace. Still others grow very rapidly; horses are fully grown in less than two years, and aquatic whales can reach 50 to 100 tonnes in just a few decades. Bull elephants take about 30 years to mature. All living birds grow rapidly; this is especially true of altricial species and of the big ratites. No extant bird takes more than a year to grow up, but some of the recently extinct giant island ratites may have taken a few years to complete growth. The secret to fast growth appears to be having an aerobic capacity high enough to allow the growing juvenile, or its adult food provider, to gather the large amounts of food needed to sustain rapid growth.

High mortality rates from predation, disease, and accidents make it statistically improbable that unarmored, nonaquatic animals will live very long lives, so they are under pressure to grow rapidly. On the other hand, starting to reproduce while still growing tends to slow down the growth process as energy and nutritional resources are diverted to produce offspring. Few mammals and no living birds begin to breed before they reach adult size. No bird continues to grow once it is mature. Nor do most mammals, but some marsupials and elephants never quite cease growing.

At the microscopic scale the bone matrix is influenced by the speed of growth, and the bone matrix of dinosaurs tended to be more similar to that of birds and mammals, which grows at a faster pace than that of reptiles. Bone ring counts are being used to estimate the growth rate and life span of a growing number of extinct dinosaurs, but this technique can be problematic because some living birds lay down more than one ring in a year, so ring counts can overestimate age and understate growth rate. There is also the problem of animals that do not lay down growth rings; it is probable that they grow rapidly, but exactly how fast is difficult to pin down. There are additional statistical issues, because as animals grow the innermost growth rings tend to be destroyed, leading to difficulties in estimating the number of missing age markers. Almost all dinosaurs sampled so far appear to have grown at least somewhat faster than land reptiles. A possible exception is a very small, birdlike troodont theropod whose bone rings seem to have been laid down multiple times in a year, perhaps because it was reproducing while growing. The earliest, smallest armored dinosaurs look like they were in the reptilian growth zone, like some mammals. Most small dinosaurs fall along the lower end of the mammalian zone of growth, perhaps because they were reproducing while immature. Rates of growth were variable in prosauropods, as was final adult size to a remarkable degree. Most gigantic dinosaurs appear to have grown as fast as similar-sized land mammals, with the hadrosaurs and ceratopsids—which did not lay down growth rings when juveniles—apparently being particularly quick to mature for the group. Some giant sauropods appear to have grown with the spectacular swiftness seen in the big rorqual whales, getting to full size in a few decades (note that a *Jurassic Park* scenario flaw as little noticed as it is glaring is the presence of giant artificially bred dinosaurs so soon after the initiation of the paleozoo project). The growth achievement of



Comparison of growth between same-scale 6-tonne African elephant and 80-tonne titanosaur

the greatest sauropods is astonishing. Giant mammals get a head start, being born as large calves only a few dozen times smaller than the adults, and then being nourished with enormous amounts of nutrient-dense milk. Hatchling sauropods had to expand their mass tens of thousands of times in just a few decades and with little or no nourishment provided by the adults. Armored dinosaurs appear to have grown less quickly than the others.

The cessation of significant growth of the outer surface of many adult dinosaur bones indicates that most but not all species did not grow throughout life. Medium-sized and large mammals and birds live for only a few years or decades, elephants live about half a century, and giant whales can last longer, with the sluggish rights making it well over 100 years. There is no evidence that dinosaurs lived longer than mammals or birds of similar size. Living in the fast lane, tyrannosaurs combined rapid growth with rather short life spans of 20 to 30 years. Other giant theropods did not grow as extremely fast and lived longer, up to half a century. Sauropods seem to have enjoyed similarly long life spans—whether they made it to a full century or beyond is not documented, but this would not be surprising in the case of the biggest examples. If they did, they may have matched the life spans of much smaller giant tortoises.

ENERGETICS

Vertebrates can utilize two forms of power production. One is aerobiosis, the direct use of oxygen taken in from the lungs to power muscles and other functions. Like air-breathing engines, this system has the advantage of producing power indefinitely but is limited in its maximum power output. An animal that is walking at a modest speed for a long distance, for instance, is exercising aerobically. The other is anaerobiosis, in which chemical reactions that do not immediately require oxygen are used to power muscles. Rather like rockets that do not need to take in air, this system has the advantage of being able to generate about 10 times more power per unit of tissue and time. But it cannot be sustained for an extended period and produces toxins that can lead to serious illness if sustained at too high a rate for too long, which is tens of minutes. Anaerobiosis also builds up an oxygen debt that has to be paid back during a period of recovery. Any fairly fast animal that is running, swimming, or power flying near its top speed is exercising anaerobically.

Most fish and all amphibians and reptiles have low resting bradymetabolic rates and low aerobic capacity. They are therefore bradyenergetic, and even the most energetic reptiles, including the most aerobically capable monitor lizards, are unable to sustain truly high levels of activity for extended periods. Many bradyenergetic animals are, however, able to achieve very high levels of anaerobic burst activity, such as when a monitor lizard or crocodilian suddenly dashes toward and captures prey. Because bradyenergetic animals do not have high metabolic rates, they are largely dependent on external heat sources, primarily the ambient temperature and the sun, for their body heat, so they are ectothermic. As a consequence, bradyenergetic animals tend to experience large fluctuations in body temperature, rendering them heterothermic. The temperature at which reptiles normally operate varies widely depending on their normal habitat. Some are adapted to function optimally at modest temperatures of 12°C (52°F). Those living in hot climates are optimized to function at temperatures of 38°C (100°F) or higher, so it is incorrect to generalize reptiles as "cold blooded." In general, the higher the body temperature is, the more active an animal can be, but even warm reptiles have limited activity potential.

Most mammals and birds have high resting tachymetabolic rates and high aerobic capacity. They are therefore tachyenergetic and are able to sustain high levels of activity for extended periods. The ability to better exploit oxygen for power over time is probably the chief advantage of being tachyenergetic. Tachyenergetic animals also use anaerobic power to briefly achieve the highest levels of athletic performance, but they do not need to rely on this as much as reptiles, are not at risk of serious self-injury, and can recover more quickly. Because tachyenergetic animals have high metabolic rates, they produce most of their body heat internally, so they are endothermic. As a consequence, tachyenergetic animals can achieve more stable body temperatures. Some, like humans, are fully homeothermic, maintaining a nearly constant body temperature at all times when healthy. Many birds and mammals, however, allow their body temperatures to fluctuate to varying degrees, for reasons ranging from going into some degree of torpor to storing excess heat on hot days, on a daily or seasonal basis. So they are semiheterothermic or semihomeothermic depending on the degree of temperature variation. The ability to keep the body at or near its optimal temperature is another advantage of having a high metabolic rate. Normal body temperatures range from 30°C to 44°C (86°F–105°F), with birds always at least 38°C. High levels of energy production are also necessary to do the cardiac work that creates the high blood pressures needed to be a tall animal.

Typically, mammals and birds have resting metabolic rates and aerobic capacities about 10 times higher than those of reptiles, and differences in energy budgets are even higher. However, there is substantial variation from these norms in tachyenergetic animals. Some mammals, among them monotremes, some marsupials, hedgehogs, armadillos, sloths, and manatees, have modest levels of energy consumption and aerobic performance, in some cases not much higher than those seen in the most energetic reptiles. In general, marsupials are somewhat less energetic than their placental counterparts, so kangaroos are about a third more energy

efficient than deer. Among birds, the big ratites are about as energy efficient as similar-sized marsupials. At the other extreme, some small birds share with similarly tiny mammals extremely high levels of oxygen consumption even when their small body size is taken into account.

Widely different energy systems have evolved because they permit a given species to succeed in its particular habitat and lifestyle. Reptiles enjoy the advantage of being energy efficient, allowing them to survive and thrive on limited resources. Tachyenergetic animals are able to sustain much higher levels of activity that can be used to acquire even more energy that can then be dedicated to the key factor in evolutionary success, reproduction. Tachyenergy has allowed mammals and birds to become the dominant large land animals from the tropics to the poles. But reptiles remain very numerous and successful in the tropics and, to a lesser extent, in the temperate zones.

As diverse as the energy systems of vertebrates are, there appear to be things that they cannot do. All insects have low, reptilelike resting metabolic rates. When flying, larger insects use oxygen at very high rates similar to those of birds and bats. Insects can therefore achieve extremely high maximal/minimal metabolic ratios, allowing them to be both energy efficient and aerobically capable. Insects can do this because they have a dispersed system of tracheae that oxygenate their muscles. No vertebrate has both a very high aerobic capacity and a very low resting metabolism, probably because the centralized respiratory-circulatory system requires that the internal organs work hard even when resting in tachyenergetic vertebrates. An insect-like metabolic arrangement should not, therefore, be applied to dinosaurs. However, it is unlikely that all the energy systems that have evolved in land vertebrates have survived until today, so the possibility that some or all dinosaurs were energetically exotic needs to be considered.

The general assumption until the 1960s was that dinosaur energetics was largely reptilian, but most researchers now agree that their power production and thermoregulation were closer to those of birds and mammals. It is also widely agreed that because dinosaurs were such a large group of diverse forms, there was considerable variation in their energetics, as there is in birds and especially mammals.

Reptiles' nonerect, sprawling legs are suitable for the slow walking speeds of 1–2 km/h (0.5–1 mph) that their low aerobic capacity can power over extended periods. Sprawling limbs also allow reptiles to easily drop onto their belly and rest if they become exhausted. No living bradyenergetic animal has erect legs. Walking is always energy expensive—it is up to a dozen times more costly than swimming the same distance—so only aerobically capable animals can easily walk faster than 3 km/h. The long, erect legs of dinosaurs matched those of birds and mammals and favored the high walking speeds of 3–10 km/h (2–6 mph) that only tachyenergetic animals can sustain for hours at a time. The speed at which an animal of a given size is moving can be approximately estimated from the length of its stride—an animal that is walking slowly steps with shorter strides than it does when it picks up the pace. The trackways of a wide variety of dinosaurs show that they normally walked at speeds of over 3 km/h, much faster than the slow speeds recorded in the trackways of prehistoric reptiles. Dinosaur legs and the trackways they made both indicate that the dinosaurs' sustained aerobic capacity exceeded the reptilian maximum.

Even the fastest reptiles have slender leg muscles because their low-capacity respirocirculatory systems cannot supply enough oxygen to a larger set of locomotory muscles. Mammals and birds tend to have large leg muscles that propel them at a fast pace over long distances. As a result, mammals and birds have a large pelvis that supports a broad set of thigh muscles. It is interesting that protodinosaurs, the first theropods, and the prosauropods had a short pelvis that could have anchored only a narrow thigh. Yet their legs are long and erect. Such a combination does not exist in any modern animal. This suggests that the small-hipped dinosaurs had an extinct metabolic system, probably intermediate between those of reptiles and mammals. All other dinosaurs had the large hips able to support the large thigh muscles typical of more aerobically capable animals. Among the big-hipped dinosaurs, the relatively sluggish therizinosaurs, stegosaurs, and armored ankylosaurs were likely to have had lower energy budgets than their faster-moving relatives.

That many dinosaurs could hold their brains far above the level of their hearts indicates that they had the high levels of power production seen in similarly tall birds and mammals. This would have been especially true of the ultratall sauropod giants. Just how much so is, however, a matter of question because it is not certain whether extra-tall creatures are stuck with just using ever higher blood pressures to push blood many meters above heart level, or whether they can utilize a siphon effect to partly reduce the vertical loads in the blood column. Some work on giraffes suggests the latter is operative to some level, but further research awaits.

It has long been questioned, incorrectly, how high-metabolism sauropods could have fed themselves with the small heads that made their long necks possible. The small head of a sauropod was like the small head of a tachyenergetic emu or ostrich—it was basically all mouth. Most of the head of herbivorous mammals consists of the dental batteries they use to chew food after it has been cropped with the mouth, which is restricted to the front end of the jaw. Also, sauropod heads are not as small as they look—the mouths of the biggest sauropods could engulf the entire head of a giraffe. The breadth of the sauropod mouth is the same as that of herbivorous mammals of the same body mass. If a tachyenergetic sauropod of 50 tonnes ate as much as expected in a mammal of its size, then it needed to consume over half a tonne of fresh fodder a day. But that is only 1 percent of its own body mass, and if the sauropod fed for 14 hours each day and took one bite per minute, then it needed to bite off only about half a kilogram of plant material each time.

That would have been easy for the sauropod's head, which weighed as much as a human body and had a mouth about 0.5 m (1.5 ft) wide. As far as big-headed dinosaurs, the sophisticated dental batteries of ceratopsids and hadrosaurs, being very similar to those of herbivorous mammals with similar chewing complexes, presumably likewise evolved to facilitate feeding a high level of energy turnover.

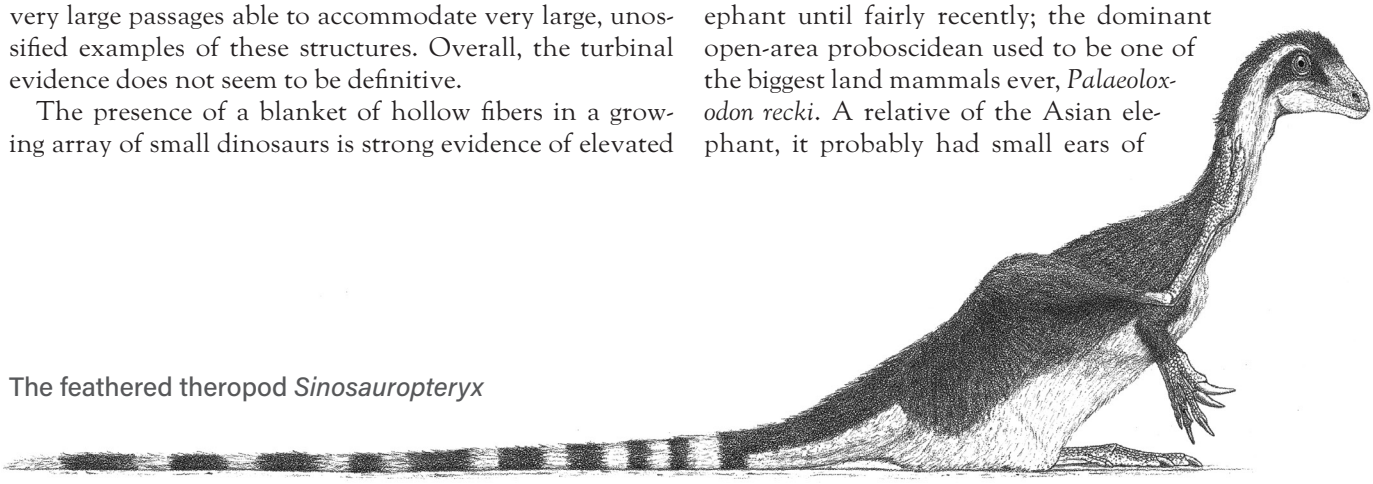
If we turn from eating to breathing, an intermediate metabolism is compatible with the unsophisticated lungs that protodinosaurs, early theropods, and prosauropods appear to have had. Too little is known about the respiration of ornithischians to relate it to metabolic level, except that the possible presence of a mammal-like diaphragm in ornithopods hints that they had a mammalian level of oxygen intake. The highly efficient, birdlike, air sac–ventilated respiratory complex of avepod theropods and sauropods is widely seen as evidence that elevated levels of oxygen consumption evolved in these dinosaurs. Sauropods probably needed a birdlike breathing complex in order to oxygenate a high metabolic rate through their long tracheae. Some reptiles with low energy levels had long necks, some marine plesiosaurs among them, but because they had low metabolic rates, they did not need air sacs to help pull large volumes of air into their lungs.

Many birds and mammals have large nasal passages that contain respiratory turbinals. These are used to process exhaled air in a manner that helps retain heat and water that would otherwise be lost during the high levels of respiration associated with high metabolic rates. Because they breathe more slowly, reptiles do not need or have respiratory turbinals. Some researchers point to the lack of preserved turbinals in dinosaur nasal passages, and the small dimensions of some of the passages, as evidence that dinosaurs had the low respiration rates of bradyenergetic reptiles. However, some birds and mammals lack well-developed respiratory turbinals, and in a number of birds they are completely cartilaginous and leave no bony traces. Some birds do not even breathe primarily through their nasal passages: California condors, for example, have tiny nostrils. The space available for turbinals has been underestimated in some dinosaurs, and other dinosaurs, ceratopsids most of all, had very large passages able to accommodate very large, unossified examples of these structures. Overall, the turbinal evidence does not seem to be definitive.

The presence of a blanket of hollow fibers in a growing array of small dinosaurs is strong evidence of elevated metabolic rates. Such insulation hinders the intake of environmental heat too much to allow ectotherms to quickly warm themselves and is never found adorning bradyenergetic animals. The evolution of insulation early in the group indicates that high metabolic rates also evolved near the beginning of the group or in their ancestors. The uninsulated skin of many dinosaurs is compatible with high metabolic rates, as in mammalian giants, many suids, human children, and even small naked tropical bats. The tropical climate most dinosaurs lived in reduced the need for insulation, and the bulk of large dinosaurs eliminated any need for it.

The low exercise capacity of land reptiles appears to prevent them from being active enough to gather enough food to grow rapidly. In an expression of the principle that it takes money to make money, tachyenergetic animals are able to eat the large amounts of food needed to produce the power needed to gather the additional large amounts of food needed to grow rapidly. Tachyenergetic juveniles either gather the food themselves or are fed by their parents. That dinosaurs, large and small, usually grew at rates faster than those seen in land reptiles of similar size indicates that the former had higher aerobic capacity and energy budgets.

A hot topic has been the concern by many that giant dinosaurs would have overheated in the Mesozoic greenhouse if they had avian- or mammalian-like levels of energy production. However, the largest animals dwelling in the modern tropics, including deserts, are big birds and mammals. And consider that there are no reptiles over a tonne dwelling in the balmy tropics. Further consider that some of the largest elephants live in the Namib Desert of the Skeleton Coast of southwestern Africa, where they often have to tolerate extreme heat and sun without the benefit of shade. It is widely thought that elephants use their ears to keep themselves cool when it is really hot, something dinosaurs could not do. However, elephants flap their ears only when the ambient temperature is below that of their bodies. When the air is as warm as the body, heat can no longer flow out, and flapping the ears actually picks up heat when the air is warmer than the body. Nor was the big-eared African elephant the main savanna elephant until fairly recently; the dominant open-area proboscidean used to be one of the biggest land mammals ever, *Palaeoloxodon recki*. A relative of the Asian elephant, it probably had small ears of



The feathered theropod *Sinosauropteryx*

little use for shedding body heat at any temperature. It is actually small animals that are most in danger of suffering heat exhaustion and heat stroke because their small bodies pick up heat from the environment very quickly. The danger is especially acute in a drought, when water is too scarce to be used for evaporative cooling. Because they have a low surface area/mass ratio, large animals are protected by their bulk against the high heat loads that occur on very hot days, and they can store the heat they generate internally. Large birds and mammals retain the heat they produce during the day by allowing their body temperature to climb a few degrees above normal and then dumping it into the cool night sky, preparing for the cycle of the next day.

At the other end of the temperature spectrum, the presence of a diverse array of dinosaurs in temperate polar regions and highlands that are known to have experienced freezing conditions during the winter, and were not particularly warm even in the summer, provides additional evidence that dinosaurs were better able to generate internal heat than reptiles, which were scarce or totally absent in the same habitats. It was not practical for land-walking dinosaurs to migrate far enough toward the equator to escape the cold; it would have cost too much in time and energy, and in some locations oceans barred movement toward warmer climes. The presence of sauropods in some of the wintry habitats in northern Australia and central Asia directly refutes the hypothesis that big dinosaurs used their bulk to keep warm by retaining the small amount of internal heat produced by a reptilian metabolism; only a higher level of energy generation could have kept the body core balmy and the skin from freezing. The discovery of probable dinosaur burrows in then-polar Australia suggests that some small dinosaurs did hibernate through the winter in a manner similar to bears. At the other end of the size spectrum, sauropods are missing from the most extreme polar regions, probably because the cold, dark winters left them without enough food to power their titanic bodies.

Bone isotopes have been used to help assess the metabolism of dinosaurs. These can be used to examine the temperature fluctuations that a bone experienced during life. If the bones show evidence of strong temperature differences, then the animal was heterothermic on either a daily or seasonal basis. In this case the animal could have been either a bradyenergetic ectotherm or a tachyenergetic endotherm that hibernated in the winter. The results indicate that most dinosaurs, large and small, were more homeothermic, and therefore more tachyenergetic and endothermic, than crocodilians from the same formations. An ankylosaur shows evidence of being heterothermic. Because the armored dinosaur lived at a high latitude, it is possible that it hibernated in the dark winter, perhaps bedding down in dense brush where it was protected by its armor against the chill as well as predators.

Bone biomolecules too are being used to restore the metabolic rates of dinosaurs. This effort is in its early stages, and it is not clear that the sample of living and fossil animals of known metabolic levels is yet sufficient to establish the reliability of the method. And the sample of dinosaurs is also too limited to allow high confidence in the results to date. This is all the more true because the estimates for dinosaurs appear inconsistent in peculiar ways. While the one armored ankylosaur is attributed with a high energy budget that appears excessive for such a relatively slow-moving creature with weak dentition, the sole armored stegosaur is recovered well down in the reptilian range, which looks both too low for an animal with long, erect legs and fairly fast growth and too different from the other armored dinosaur. Also problematic is that reptilian energetics are assigned to the hadrosaur and the ceratopsid examined, not the higher levels expected in animals with such fast food processing and growth that have the large leg muscles and fast walking pace expected in tachyenergetic endotherms. Also of note is the low metabolism of the giant flying marine pterosaur. The initial biomolecule results indicating that the earliest dinosaurs were endotherms, with theropods and sauropods great and small remaining so, while some ornithischians irregularly reverted to bradyenergetic ectothermy, await further analysis.

Because the most basal and largest of living birds, the ratites, have energy budgets similar to those of marsupials, it is probable that most dinosaurs did not exceed this limit. This fits with some bone isotope data that seem to indicate that dinosaurs had moderately high levels of food consumption, somewhat lower than seen in most placentals of the same size. Possible exceptions are the tall sauropods with their high circulatory pressures, and polar dinosaurs that remained active in the winter and needed to produce lots of warmth. At the opposite extreme, early dinosaurs, slower-growing and slower-moving armored forms, and the awkward therizinosaurs probably had modest energy budgets like those of the less-energetic mammals. It is likely that dinosaurs, like birds, were less prone to controlling their body temperatures as precisely as do many mammals. This is in accord with their tendency to lay down bone rings. Because they lived on a largely hot planet, it is probable that most dinosaurs had high body temperatures of 38°C or more to be able to resist overheating. The possible exception was again high-latitude dinosaurs, which may have adopted slightly lower operating temperatures and saved some energy, especially if they were active during the winter. Some researchers have characterized dinosaurs as mesotherms intermediate between reptiles on the one hand and mammals and birds on the other. But because some mammals and birds themselves are metabolic intermediates, and dinosaurs were probably diverse in their energetics, with some in the avian-mammalian zone, it is not appropriate to tag dinosaurs with a uniform, intermediary label.

Until the 1960s it was widely assumed that high metabolic rates and/or endothermy were an atypical specialization among animals, being limited to mammals and birds,

perhaps some therapsid ancestors of mammals, and the flying pterosaurs. The hypothesis was that being tachyenergetic and endothermic is too energy expensive and inefficient for most creatures and evolved only in special circumstances such as the presence of live birth and lactation, or powered flight. Energy efficiency should be the preferred status of animals, as it reduces their need to gather food in the first place. Since then it has been realized that varying forms of tachyenergy definitely are or probably were present in large flying insects, some tuna and lamnid sharks, some basal Paleozoic reptiles, some marine turtles and the oceangoing plesiosaurs, ichthyosaurs, and mosasaurs, brooding pythons, basal archosaurs, basal crocodilians, pterosaurs, all dinosaurs including birds, some pelycosaurs, therapsids, and mammals. Energy-expensive elevated metabolic rates and body temperatures appear to be a widespread adaptation that has evolved multiple times in animals of the water, land, and air. This should not be surprising in that being highly energetic allows animals to do things that bradyenergetic ectotherms cannot do, and DNA selection acts to exploit available lifestyles that allow reproductive success without a priori caring whether it is done energy efficiently or not. Whatever works, works. So many animals do live on low, energy-efficient budgets, while others follow the scheme of using more energy to acquire yet more energy that can be dedicated to reproducing the species.

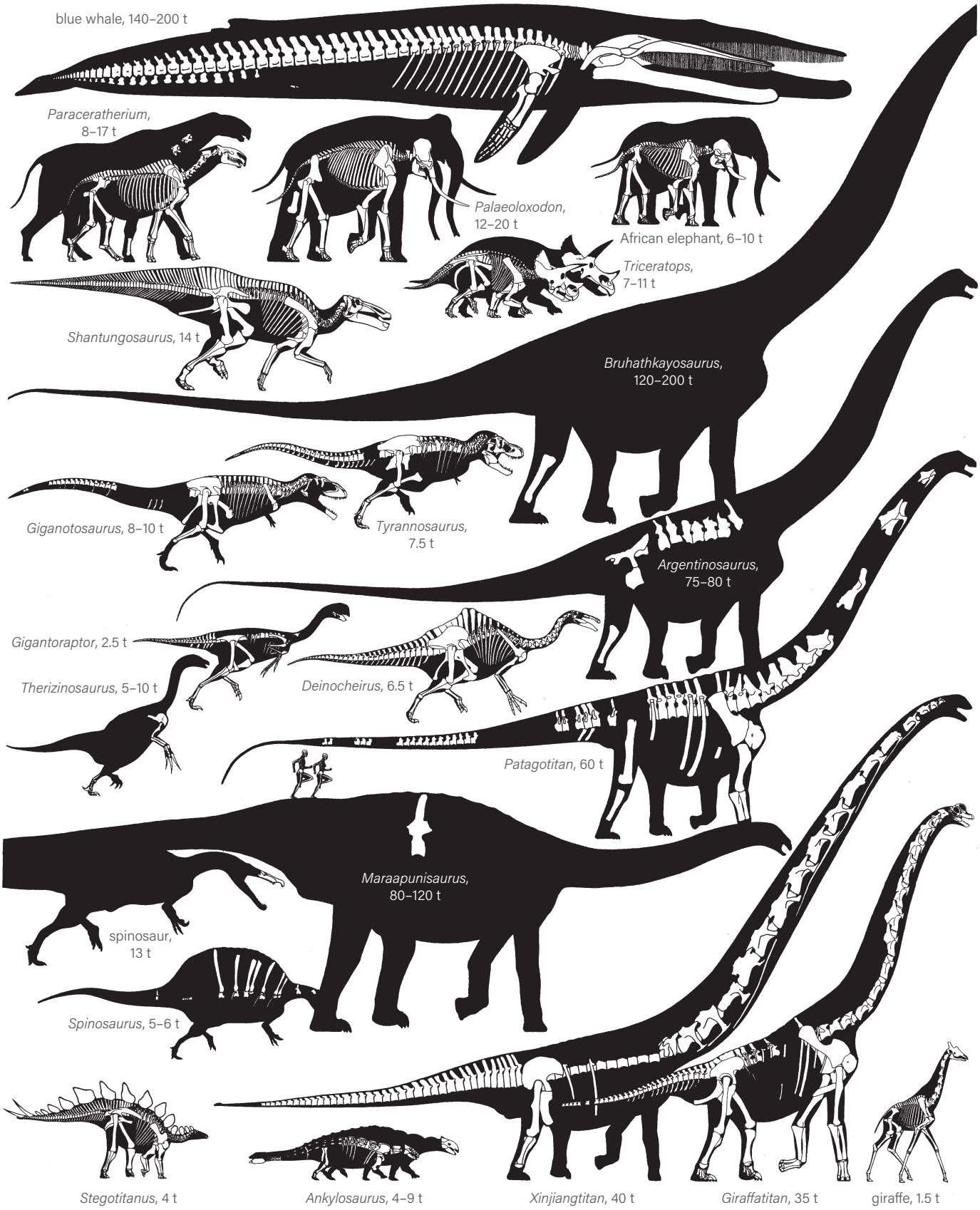
A long-term debate asks what specifically it is that leads animals to be tachyenergetic and endothermic. One hypothesis proposes that it is habitat expansion, that animals able to keep their bodies warm when it is cold outside are better or exclusively able to survive in chilly places—near the poles, at high altitudes, in deep waters—or during frosty nights. The other proffers that only tachyenergetic animals with high aerobic capacity can achieve high levels of sustained activity regardless of the ambient temperature, whether at sea level in the tropical daylight, or during polar winter nights, and that ability is critical to going high energy. Certainly the first hypothesis is true, but it is also true that all of the many animal groups that feature high energy budgets and warmer-than-ambient body temperatures also thrive in warm and even hot climes, where they beat out the bradyenergetic creatures in activity levels. So both hypotheses are operative, and which is more so depends on the biocircumstances—including being really big on land.

GIGANTISM

Although dinosaurs evolved from small protodinosaurs, and many were small—birds included—dinosaurs are famous for their tendency to develop gigantic forms. The average mammal is the size of a dog, whereas the average fossil dinosaur was bear sized. But those are just averages. Predatory theropods reached as much as 10-plus tonnes, as big as elephants and dwarfing the largest carnivorous mammals by a factor or 10 or more. Sauropods exceeded the size of the largest land mammals, mammoths, and the long-legged paracerathere rhinos of 15 to 20 tonnes by a factor of at least four to five and apparently matched the most massive whales.

Among land animals whose energetics are known, only those that are tachyenergetic have been able to become gigantic on land. The biggest fully terrestrial reptiles, some oversized tortoises and monitors, have never much exceeded a tonne. Land reptiles are probably not able to grow rapidly enough to reach great size in reasonable time. Other factors may also limit their size. It could be that living at 1 g, the normal force of gravity, without the support of water, is possible only among animals that can produce high levels of sustained aerobic power. The inability of the low-power, low-pressure reptilian circulatory system to pump blood far above the level of the heart probably helps limit the size of bradyenergetic land animals. That a number of Mesozoic dinosaurs, including those that were predaceous, exceeded a tonne, as have mammals since then, is compelling evidence that they too had high aerobic power capacity and correspondingly elevated energy budgets. The ultimate example of great height driven by elevated metabolics is seen in ultratall sauropods. Their extreme height indicates that their hearts could push blood many meters up against the gravity well at pressures up to two or three times higher than the 200 mm Hg giraffes need to oxygenate their brains. And it is unlikely that such tall and massive animals in danger of fatal injury from falling could risk a moment of hypoxic wooziness from an oxygen-deprived brain. If so, then sauropods had hardworking hearts whose high energy demands would have required a very high level of oxygen consumption. Supertall animals would have needed, like giraffes, special vascular adaptations to cope with the problems associated with fluctuating pressures as the animal stood or lay down, and raised and lowered its head from drinking level to the maximum vertical reach.

Only sauropods have exceeded 20 tonnes on land. The question is, why that unique biological achievement? Very tall necks like those of sauropods and giraffes evolve in an evolutionary feedback loop that involves two distinct but reinforcing factors. Increasing height serves as a dominance display that enhances reproductive success by intimidating rivals and impressing mates. This is similar to other reproductive displays such as the tails of peacocks and the giant antlers of big cervids. And as the head gets higher, the herbivore also has a competitive feeding advantage over shorter herbivores in accessing the enormous food resources, in the crowns of tall trees, that provide the power source needed to pump blood to the brain, held far above the heart, that



Dinosaur giants compared with mammals

allows the animal to reach all that food. Sauropods could take this to an exceptional extreme because, lacking dental batteries and big brains, sauropod heads were relatively small, so sauropods were able to evolve extremely tall necks that in turn required enormous bodies to anchor them upon and to contain the hardworking hearts they needed. With their more toothy big heads, mammals are apparently limited to the 6 m (20 ft) height of giraffes. The tallest sauropods were able to reach up to maybe 20 m (60 ft)—without better understanding of how animals get blood really high up, it is not known whether that was the maximum animal height attainable. Also possibly helping sauropods become supersized were the pneumatic vertebrate and other air sacs that had evolved to improve respiratory capacity in tune with the high metabolic rates needed to be so tall and heavy. Those lightened the load on their bones and muscles somewhat, which could have been especially pertinent regarding the elongated necks. This option has not been available to mammals, or to ornithischian dinosaurs for that matter. But this effect should not be exaggerated, in part because recent work is showing that sauropods' internal air spaces were not as dramatically density reducing as has been widely thought.

The hypothesis that only tachyenergetic animals can grow to enormous dimensions on land is called terramegathermy. An alternative concept, gigantothermy, proposes that the metabolic systems of giant reptiles converge with those of giant mammals, resulting in energy efficiency in all giant animals. In this view, giants rely on their great mass, not high levels of heat production, to achieve thermal stability. This idea reflects a misunderstanding of how animal power systems work. A consistently high body temperature does not provide the motive power needed to sustain high levels of activity; it merely allows a tachyenergetic animal, and only an animal with a high aerobic capacity, to sustain high levels of activity around the clock. A gigantic reptile with a high body temperature would still not be able to remain highly athletic for extended periods. Measurements show that the metabolic rates and aerobic capacity of elephants and whales are as high as expected in mammals of their size and are far higher than those of the biggest crocodilians and turtles, which have the low levels of energy production typical of reptiles. Also pushing animals to be big is improved thermoregulation—the high bulk to relatively low surface area ratio making it easier to both retain internal warmth when it is chilly and keep external heat out and store heat on hot days.

Another, subtle reason that dinosaurs, particularly supersauropods and theropods, could become so enormous has to do with their mode of reproduction. Because big mammals are slow-breeding K-strategists that lavish attention and care on the small number of calves they produce, there always has to be a large population of adults present to raise the next generation. A healthy herd of elephants has about as many breeding adults as it does juveniles, which cannot survive without parental care. Because there always has to be a lot of grown-ups, the size of the adults has to be limited in order to avoid overexploiting their habitat's food resources, which will cause the population to collapse. This constraint appears to limit slow-reproducing mammalian herbivores from exceeding 10–20 tonnes. Flesh eaters live off an even smaller resource base because they prey on the surplus herbivores, and it seems that carnivorous mammals cannot maintain a viable population if they are larger than between half a tonne and 1 tonne.

Because giant dinosaurs were fast-breeding r-strategists that produced large numbers of offspring that could care for themselves, their situation was very different from that of big mammals. A small population of adults was able to produce large numbers of young each year. Even if all adults were killed off on occasion, their eggs and offspring could survive and thrive, keeping the species going over time. Because dinosaurs could get along with smaller populations of adults, the grown-ups were able to grow to enormous dimensions without overexploiting their resource base. This evolutionary scheme allowed plant-eating dinosaurs to grow to over 20 to perhaps on occasion 200 tonnes. It is notable that supersauropod fossils are particularly rare, indicating small populations. Because the bulk of the biomass of adult herbivorous dinosaurs was tied up in oversized giants, the theropods needed to evolve great size themselves in order to be able to fully access the nutrition tied up in the huge adults—the idea that theropods grew to 6 to 10 tonnes only to "play it safe" by consistently hunting smaller juveniles is not logical—and the fast-breeding and fast-growing predators could reach tremendous size. The existence of oversized predators in turn may have resulted in a size race in which sauropods evolved great size in part as protection against their enemies, which later encouraged the appearance of supersized theropods that could bring them down.

It is as common as it is seemingly logical to think that being titanic in water—it being buoyant—is easier than dwelling under the full force of planetary gravity on land. But paleohistory indicates otherwise. Really big whales did not exist until very recently. For over 30 million years most or all whales were not all that big, rarely if ever exceeding around 20 tonnes. It was under the unusual conditions of ice age oceans in which cold water currents spurred higher levels of food productivity, plankton particularly, that the super baleen whales of 50–200 tonnes suddenly appeared. Back in the warm seas of the Mesozoic, reptiles and fish reached only 20 to perhaps 30 tonnes. Before the Pleistocene ocean chill, the biggest fish were 50-tonne supersharks like megalodon. In comparison, 50–200-tonne supersauropods were wandering about Mesozoic continents from the Late Jurassic to the very end of the era with little or no interruption for around 90 million years. The extra-tall land giants had the size-sustaining advantage that there were always forests full of calorie-packed big trees, a few trillion of them, to grow titanic on—until K/Pg events suddenly wrecked those forests and the equitable climate across the globe. With no small-headed dinosaurian herbivores to

regain whalelike bulk and multistory height on land, land mammals have proven unable to reach a couple dozen tonnes.

In the 1800s Edward Cope proposed what has become known as Cope's Rule, the tendency of animal groups to evolve gigantism. The propensity of dinosaurs to take this evolutionary pattern to an extreme means that the Mesozoic saw events on land that are today limited to the oceans. In modern times combat between giants occurs between orcas and whales. In the dinosaur era it occurred between orca-sized theropods and whale-sized sauropods, hadrosaurs, and ceratopsids.

MESOZOIC OXYGEN

Oxygen was absent from the atmosphere for much of the history of the planet, until the photosynthesis of single-celled plants built up enough oxygen to overwhelm the processes that tend to bind it to various elements such as iron. Until recently it was assumed that oxygen levels then became stable, making up about a fifth of the air for the last few hundred million years. Of late it has been calculated that oxygen has fluctuated strongly since the late Paleozoic. The problem is that the results are themselves variable. They do agree that the oxygen portion of the atmosphere soared to about a never-seen-again third or more during the late Paleozoic, when the great coal forests were forming and, because of the high oxygen levels, often burning. It is notable that this is when many insects achieved enormous dimensions by the standards of the group, including dragonfly relatives with wings over 0.5 m (2 ft) across. Because insects bring oxygen into their bodies by a dispersed set of tracheae, the size of their bodies may be tied to the level of oxygen.

But in the Mesozoic the situation is less clear. Oxygen levels may have plunged precipitously, sinking to a little over half the current level by the Triassic and Jurassic. In this case oxygen availability at sea level would have been as poor as it is at high altitudes today. Making matters worse were the high levels of carbon dioxide. Although not high enough to be directly lethal, the combination of low oxygen and high carbon dioxide would have posed a serious respiratory challenge that could have propelled evolution of the efficient air sac respiration of pterosaurs and some dinosaurs. But other work indicates that oxygen did not plunge so sharply, and in one analysis it never even fell below modern levels, being somewhat higher in most of the era. Reliably assaying the actual oxygen content of the atmosphere in the dinosaur days remains an important challenge.

THE EVOLUTION—AND LOSS—OF AVIAN FLIGHT

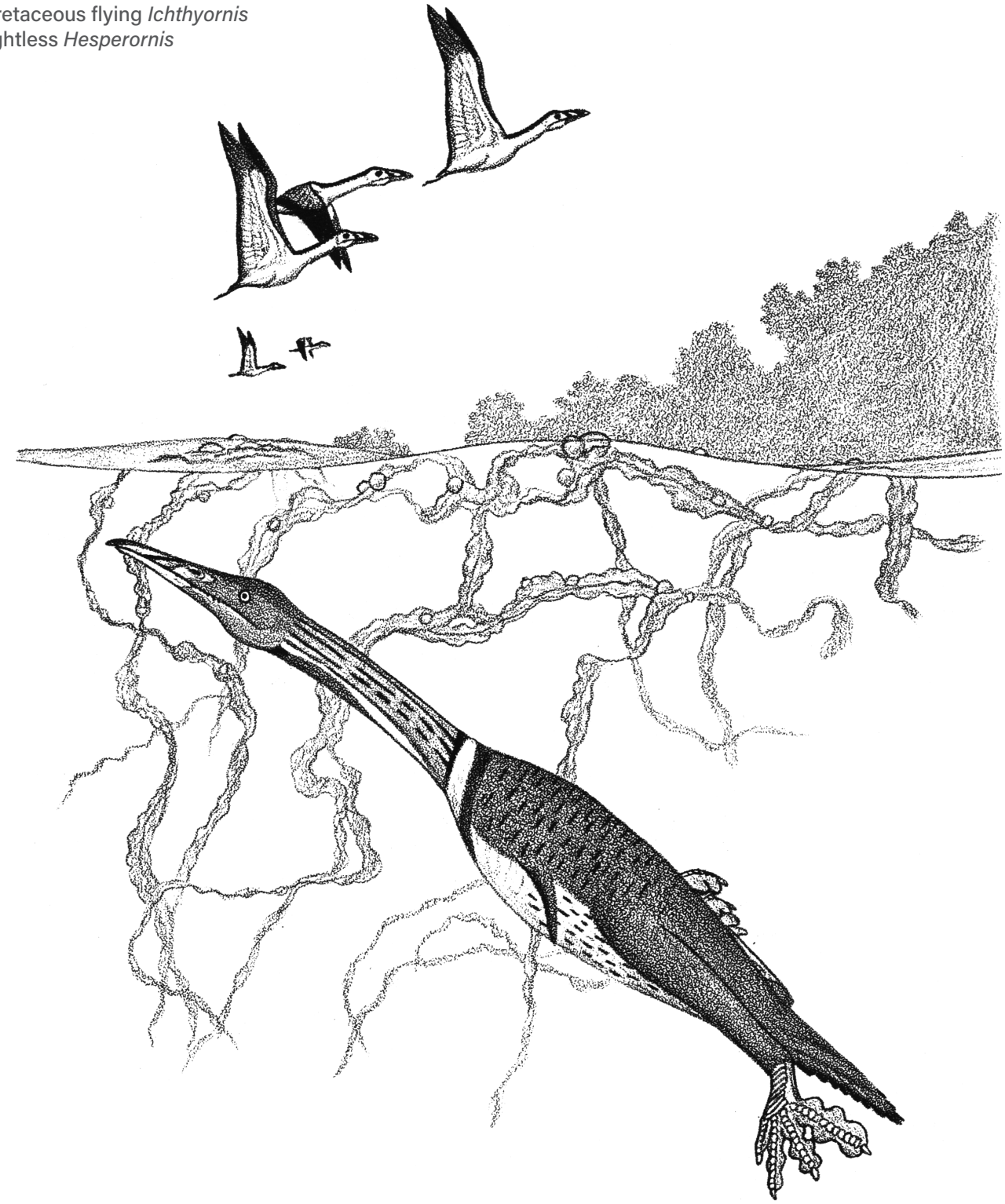
Powered flight has evolved repeatedly among animals, including numerous times in insects in the late Paleozoic and three times in tetrapods—pterosaurs in the Triassic, birds in the Jurassic, and bats in the early Cenozoic. In all cases among vertebrates, flight evolved rapidly by geological terms, so much so that the earliest stages have not yet been found in the fossil record for pterosaurs and bats. The means by which flight evolved in pterosaurs remains correspondingly obscure, although their having wing membranes attached to their legs favors it starting out as arboreal gliding. The fact that bats evolved from tiny insectivorous mammals, and the recent discovery of an early fossil bat with wings smaller than those of more modern forms, show that mammalian flight evolved in high places.

The origin of birds and their flight is much better understood than it is for pterosaurs and bats. This knowledge extends back to the discovery of Late Jurassic *Archaeopteryx* in the mid-1800s and is rapidly accelerating with the abundant new fossils that have come to light in recent years, especially from the Early Cretaceous, and from the middle of the Jurassic before *Archaeopteryx*. We can conclude that dinosaurian flight was not yet developing in the Triassic because while sediments from that time preserve an array of flying insects and early pterosaurs, nothing dinoavian has shown up. However, a major fossil gap exists because little is known about what was happening in the Early Jurassic and most of the middle of that era. Also hindering greater understanding is that the fine-grained deposits that best preserve small flying creatures are largely limited to a few geographic locations, mainly northeast China in the Middle Jurassic and Early Cretaceous and Europe in the Late Jurassic, and it is unknown what was happening in the rest of the world.

When it was assumed that birds did not evolve from dinosaurs, it was correspondingly presumed that their flight evolved among climbers that first glided and then developed powered flight. This has the advantage of our knowing that arboreal animals can evolve powered flight with the aid of gravity, as bats almost certainly did, and probably pterosaurs too. When it was realized that birds descended from deinonychosaurs, many researchers switched to the hypothesis that running dinosaurs learned to fly from the ground up. This has the disadvantage of uncertainty over whether it is practical for tetrapod flight to evolve among ground runners working against gravity.

The characteristics of birds indicate that they evolved from dinosaurs that had first evolved as bipedal runners and then evolved into long-armed climbers. If the ancestors of birds had been entirely arboreal, then they should have been semiquadrupedal forms whose sprawling legs were integrated into the main airfoil, as in bats. That birds

Late Cretaceous flying *Ichthyornis* and flightless *Hesperornis*



are bipeds whose erect legs are separate from the wings indicates that their ancestors evolved to run. Conversely, how and why ground animals would directly develop the long, strongly muscled arms and wings necessary for powered flight has not been adequately explained. The hypothesis that running theropods developed the ability to fly as a way to enhance their ability to escape up tree trunks itself involves a degree of arboreality. Small theropods, with their grasping hands and feet, were inherently suited for climbing. Some avepod theropods show specializations for climbing, especially scansoriopterygids, *Xiaotingia*, *Archaeopteryx*, and microraptorine dromaeosaurs.

Avian flight may have evolved among predatory dinosaurs that spent time both on the ground and in the trees,

with long arms that facilitated the latter. Leaps between branches could have been lengthened by developing aerodynamically asymmetrical pennaceous feathers that turned the leaps into short glides. As the feathers lengthened, they increased the length of the glides. When the protowings became large enough, flapping would have added power, turning the glides into a form of flight. The same flapping motion would have aided the rapid climbing of trees via the air rather than scrambling up trunks and branches. Selective pressures then promoted further increases in arm muscle power and wing size until the level seen in *Archaeopteryx* was present. The flying deinonychosaur had an oversized furcula and large pectoral crest on the humerus, which supported an expanded set of muscles for flapping flight. The absence of a large sternum shows that its flight was weak by modern standards. As bird flight further developed, the sternum became a large plate like those seen in dromaeosaurs. Fixed on the rib cage with ossified sternal ribs, the plate anchored large wing-depressing muscles and later sported a keel that further expanded the flight muscles. Adaptations at and near the shoulder joint improved the ability of the wing to elevate, increasing the rate of climb in flight. At the same time, the hand was stiffened and flattened to better support the outer wing primaries, and the claws were reduced and lost. The tail rapidly shortened in most early birds until it was a stub. This means that birds quickly evolved a dynamic form of flight, much more rapidly than pterosaurs, which retained a long tail stabilizer through most of the Jurassic. The above adaptations were appearing in Early Cretaceous birds, and the essentially modern flight system had evolved by the Early Cretaceous.

For all its advantages, flight has its downsides, including all the energy that is absorbed by the oversized wing tissues, especially the enormous flight muscles. Nor can flying birds be especially large. A number of derived birds with clawless hands have lost flight even on the continents, and dinobirds with only modest flight abilities and clawed hands that could be used for multiple purposes would have been more prone to losing the ability to take to the air. Yet the conventional view of dinoavian evolution does not include a single case of the loss of flight outside birds proper. This scenario is critically flawed because the possibility that weak early fliers rarely if ever lost flight over the nearly 100 million years of the Late Jurassic and Cretaceous is not viable; it would have been happening all the time. After all, continental tetrapods have undergone the massive reversals needed to again become flippered marine swimmers numerous times, and losing flight is much easier and simpler to do. Reversals both modest and radical are frequent features of Darwinian evolution.

Functional anatomical evidence for the loss of flight includes the presence in nonfliers of flight features that are normally retained in neoflightless birds. These include large squarish sternal plates supported by bony sternal ribs; bony uncinate processes on the ribs; strong flexion between horizontal, strap-shaped scapula blades strongly flexed relative to the vertical; elongated coracoids; folding arms; a number of details of the hand including stiffening and fusing of elements; bird/pterosaur/bat-style propatagium airfoil surfaces stretching from shoulder to wrist forward of the elbow; and stiffened, slender, pterosaur-like or very short birdlike tails. All these adaptations are needed for dinosaur fight, and attempts to explain them as exaptations before the evolution of flight are at best speculative. Many of these attributes apply to nonflying dromaeosaurs, whose early examples appear to have been better adapted for flight than *Archaeopteryx*. The small-armed dromaeosaurs were almost certainly neoflightless, like big ground birds. *Anchiornis* suggests that deinonychosaurs began to lose flight in the Late Jurassic, with troodonts their possible neoflightless evolutionary offspring. Therizinosaurs and oviraptorosaurs show many of the anatomical signs that some level of flight was present early in their evolution. It is particularly telling that the early flying jeholornithiform birds and flightless therizinosaurs shared strikingly similar skulls, as did in turn the deeply parrot-beaked omnivoropterygid birds and oviraptorosaurs. Such deep convergence happening once, as the conventional scenario proposes, is not likely, and it happening twice is a real evolutionary stretch. Very close relationships, in both cases involving the loss of flight expected to spawn off from such crude fliers, are the superior bioevolutionary scenario. That it turns out that basal oviraptorosaurs had retroverted pubes like flying protobirds is further evidence their ancestors once flew Mesozoic skies. The alvarezsaurs are another potential neoflightless clade. In the Cretaceous, birds themselves lost flight on occasion, most famously the widely distributed marine hesperornithiform divers, as well as some chicken- to ratite-sized European birds of uncertain relationships known from near the end of the period.

DINOSAUR SAFARI

Assume that a practical means of time travel has been invented, and, *The Princeton Field Guide to Dinosaurs* in hand, you are ready to take a trip to the Mesozoic to see the dinosaurs' world. What would such an expedition be like? Here we ignore the classic time paradox issue that plagues the very concept of time travel. What would happen if a time traveler to the dinosaur era did something that changed the course of events to such a degree that humans never evolved to travel back in time and disrupt the timeline in the first place?

One difficulty that might arise could be the lack of modern levels of oxygen and/or extreme greenhouse levels of carbon dioxide (which can be toxic for unprepared animals), especially if the expedition traveled to the Triassic or Jurassic. Acclimation could be necessary, and even then,

supplemental oxygen might be needed at least on an occasional basis. Work at high altitudes would be especially difficult. But, as noted earlier, oxygen deprivation may not have been the case. Another problem would be the high levels of heat chronically present in most dinosaur habitats. Relief would be found at high latitudes, as well as on mountains.

If the safari went to one of the classic Mesozoic habitats that included gigantic dinosaurs, the biggest problem would be the sheer safety of the expedition members. The bureaucratic protocols developed for a Mesozoic expedition would emphasize safety, with the intent of keeping the chances of losing any participants to a bare minimum. Modern safaris in Africa require the presence of a guard armed with a rifle when visitors are not in vehicles in case of an attack by big cats, hippos, buffalo, rhinos, or elephants. Similar weaponry is often needed in tiger country, in areas with large populations of grizzlies, or in Arctic areas inhabited by polar bears. The potential danger level would be even higher in the presence of flesh-eating dinosaurs as big as rhinos and elephants and able to run down a human who could potentially be out of breath because of the low oxygen. It is possible that theropods would not recognize humans as prey, but it is at least as likely that they would, and the latter would have to be assumed. Aside from the desire to not kill members of the indigenous fauna, rifles, even automatic rapid-fire weapons, might not be able to reliably bring down a 5-tonne allosauroid or tyrannosaur, and heavier weapons would be impractical to carry about. Nor would the danger come from just the predators. A herd of whale-sized sauropods would pose a serious danger of trampling or impact from tails, especially if they were spooked by humans and either attacked them as a possible threat or stampeded in their direction. Sauropods would certainly be more dangerous than elephants, whose high level of intelligence allows them to better handle situations involving humans. The horned ceratopsids, even less intelligent than rhinos, and probably with the attitudes of oversized pigs, would pose another major danger. Even medium-sized dinosaurs could pose significant risks. An attack by sickle-clawed dromaeosaurs, for instance, could result in serious casualties. So could assault by a squadron of parrot-beaked peccary-like protoceratopsids. As for the pterosaurs, the giant azhdarchids are not creatures one would want to get particularly close to.

But there would be another danger that would be as small as it is big: microbes. Expedition members would be at risk of picking up exotic Mesozoic disease organisms they would not be immune to, and at least as bad would be the danger of contaminating the ancient environment with a host of late Cenozoic viruses, bacteria, and parasites that could seriously disrupt Jurassic and Cretaceous life.

The combined menaces, small and big, would mean that time-traveling dinosaur watchers would probably be banned from directly interacting with the ancient habitats. Instead of walking about under the Mesozoic sun and stars, breathing ancient fresh air, binoculars in hand, they would always have to wear microbe-proof biohazard suits when not in vehicles, and habitats would likewise need to be sealed against microbes getting in or out. Dwelling in dinosaur habitats would be a lot like living on the moon or Mars—a very artificial experience in which paleonauts would be significantly detached from the fascinating world around them, always respiring pretreated air. An advantage of being in biosuits would be temperature control, which would eliminate dealing with the extreme heat prevalent in much of the Mesozoic. Also dealt with would be issues with the composition of the atmosphere. Travel by foot would probably be largely precluded in habitats that included big theropods, sauropods, and ceratopsids. Expedition members would have to move about on the ground in vehicles sufficiently large and strong to be immune from attacks by colossal dinosaurs. Movement away from the vehicles would be possible only when drones showed that the area was safe. Even in places lacking giant dinosaurs, there would be the peril of a biosuit being breached by an assault by a smaller dinosaur—any such penetration from any cause would require some level of medical care, quarantine at least. Defensive weapons might be necessary, although pepper spray guns might suffice. Yet another danger in some Cretaceous habitats would be elephant-sized crocodilians that might snap up and gulp down whole a still-living human unwary enough to go near or in the waters where dinosaurs hung out.

A safe way to observe the prehistoric creatures would be remotely via drones that could observe the winged archosaurs when on the ground and, even better, follow them in the air. Manned ultralights would work too, although they would have their own dangers. Also relatively safe would be visiting islands too small to sustain big predators.

A consequence of time travel for paleoartists would be the obsolescence of every single dinosaur life restoration. One possible exception might be the first dinosaur proven to be feathered, little *Sinosauropteryx*, its plumage and coloration still being the best understood. Much the same for *Microraptor*.

IF DINOSAURS HAD SURVIVED

Assume that the K/Pg impact is what killed off the dinosaurs, but also assume that the impact did not occur and that nonavian dinosaurs continued into the Cenozoic. What would the evolution of land animals have been like in that case?

Although much will always be speculative, it is likely that the Age of Dinosaurs would have persisted—indeed the Mesozoic era would have endured—aborting the Cenozoic Age of Mammals. Thirty million years ago western North America probably would have been populated

by great dinosaurs rather than the rhino-like titanotheres. Having plateaued out in size for the last half of the Mesozoic, sauropods would probably not have gotten bigger, but the continuation of the ultimate browsers should have inhibited the growth of dense forests. Even so, the flowering angiosperms would have continued to evolve and to produce a new array of food sources including well-developed fruits that herbivorous dinosaurs would have needed to adapt to in order to exploit.

What is not certain is whether mammals would have remained diminutive or would have begun to compete with dinosaurs for the large-body ecological niches. By the end of the Cretaceous, sophisticated marsupial and placental mammals were appearing, and they may have been able to begin to mount a serious contest with dinosaurs as time progressed. Eventually, southward-migrating Antarctica would have arrived at the South Pole and formed the enormous ice sheets that act as a giant air-conditioning unit for the planet. At the same time, the collision of India and Asia, which closed off the once-great Tethys Ocean and built up the miles-high Tibetan Plateau, also contributed to the great planetary cool-off of the last 20 million years that eventually led to the current ice age despite the rising heat production of the sun. This should have forced the evolution of grazing dinosaurs able to crop the spreading savanna, steppe, and prairie grasslands that thrive in cooler climates. In terms of thermoregulation, dinosaurs should have been able to adapt, although growing winter food shortages may have been a problem for supersauropods. And the also energetic mammals may have been able to exploit the decreasing temperatures. Perhaps big mammals of strange varieties would have formed a mixed dinosaur-mammal fauna, with the former perhaps including some big birds. Mammals may also have proven better able to inhabit the oceans than nonavian dinosaurs, generating manatees, seals, and whales or beasts like them.

The birdlike dinosaurs evolved brains larger and more complex than those of reptiles toward the end of the Jurassic and beginning of the Cretaceous, but they never exceeded the lower avian range, and they did not exhibit a strong trend toward larger size and intricacy in the Cretaceous similar to the startling increase in neural capacity in Cenozoic mammals. We can only wonder whether dinosaurs would have eventually undergone their own expansion in brain power had they not gone extinct. Perhaps the evolution of large-bodied, big-brained mammals would have compelled dinosaurs to upgrade thinking performance as well. In such a competition, the better brain efficiency of the bird relatives might have proven an evolutionary advantage, all the more so when combined with full color vision.

The species *Homo sapiens* would not have evolved if not for the extinction of dinosaurs, but whether some form of highly intelligent, language- and tool-using animal would have developed is another matter. Modest-sized, bipedal, birdlike predatory theropods with grasping hands might have been able to do so, but the limitation to three fingers may have resulted in inferior manipulation. Or perhaps arboreal theropods with stereo color vision would have become fruit eaters whose evolution paralleled that of the increasingly brainy primates that spawned humans. Actual primates might also have appeared and evolved above the heads of the great dinosaurs, producing at some point bipedal ground mammals able to create and use tools. On the other hand, the evolution of superintelligent humans may have been a fluke and would not have been repeated in another Earthly timeline.

DINOSAUR CONSERVATION

If we take the above scenario to its extreme, assume that some group of smart dinosaurs or mammals managed to survive and thrive in a world of great predatory theropods and became intelligent enough to develop agriculture and civilization as well as an arsenal of lethal weapons. What would have happened to the global fauna?

The fate of large dinosaurs would probably have been grim. We actual humans may have been the leading factor in the extinction of a large portion of the megafauna that roamed much of the Earth toward the end of the last glacial period, and matters continue to be bad for most wildlife on land and even in the oceans. The desires and practical needs of our imaginary sapients would have compelled them to wipe out the giant theropods, whose low adult populations could have rendered them more susceptible to total loss than the not-so-big mammal carnivores. If whale-sized herbivorous dinosaurs were still extant, their low populations likely would have made them more vulnerable than elephants and rhinos. By the time the sapients developed industry, the gigantic flesh and plant eaters would probably already have been part of historical lore. If superdinosaurs had instead managed to survive in an industrial world, they would have posed insurmountable problems for zoos. Feeding lions, tigers, and bears is not beyond the means of zoos, but a single tyrannosaur-sized theropod would break the budget by consuming the equivalent of a thousand cattle-sized animals over a few decades. How could a zoo staff handle a 50-foot-tall sauropod weighing 30 or 50 tonnes or more and eating 10 times as much as an elephant?

WHERE DINOSAURS ARE FOUND

Because dinosaurs are long gone and time travel probably violates the nature of the universe, we have to be satisfied with finding the remains they left behind. With the possible exception of very high altitudes, dinosaurs lived in all places on all continents, so where they are found is determined by the existence of conditions suitable for preserving their bones and other traces, eggs and footprints especially, as well as by conditions suitable for finding and excavating the fossils. For example, if a dinosaur habitat lacked the conditions that preserved fossils, then that fauna has been totally lost. Or, if the fossils of a given fauna of dinosaurs are currently buried so deep that they are beyond reach, then they are not available for scrutiny.

All but a very small percentage of carcasses are destroyed at or soon after death. Many are consumed outright—particularly the juveniles and small adults—or in part by predators and scavengers, and almost all the rest rot or are weathered away before or after burial at some point. Even so, the number of animals that have lived over time is immense. Because at any given time a few billion dinosaurs were probably alive, mostly juveniles and small adults, and the groups existed for most of the Mesozoic, the number of dinosaur fossils that still exist on the planet is enormous, probably in the many hundreds of millions or billions of individuals.

Of these only a tiny fraction of 1 percent have been found at or near the small portion of the dinosaur-bearing formations that are exposed on the surface where the fossils can be accessed, or in the mines that allow some additional remains to be reached. Even so, the number of dinosaur fossils that have been scientifically documented to at least some degree is considerable. Some dinosaur bone beds contain the remains of thousands of individuals, and the total number of dinosaur individuals known in that sense is probably in the tens or hundreds of thousands. The question is where to find them.

Much of the surface of the planet at any given time is undergoing erosion. This is especially true of highlands. In erosional areas, sediments that could preserve the bones and other traces are not laid down, so highland faunas are rarely found in the geological record, the Yixian-Jiufotang lake-forest district being a notable exception, deposited in volcanic uplands. Fossilization has the potential to occur in areas in which sediments are being deposited quickly enough, and in large enough quantities, to bury animal remains and traces before they are destroyed by consumption or exposure. Animals can be preserved in deep fissures or caves in highland areas; this is fairly rare but not unknown when dealing with the Mesozoic. Areas undergoing deposition tend to be lowlands downstream of uplifting or volcanic highlands that provide abundant sediment loads carried in streams, rivers, lakes, or lagoons that settle out to form beds of silt, sand, or gravel. Therefore, large-scale formation of fossils occurs only in regions experiencing major tectonic and/or volcanic activity. Depositional lowlands can be broad valleys or basins of varying size in the midst of highlands, or coastal regions. As a result, most known dinosaur habitats were flatlands, usually riverine floodplains, with little in the way of local topography. In some cases the eroding neighboring highlands were visible in the distance from the locations where fossilization was occurring; this was especially true in ancient rift valleys and along the margins of large basins. The Yixian-Jiufotang did feature local volcanoes, which generally were not as common as paleoillustrators used to show them. Ashfalls can preserve skeletons en masse, but lava flows tend to incinerate and destroy animal remains. In deserts, windblown dunes preserve bones, and also when they slump when wetted by rains. Also suitable for preserving the occasional dinosaur carcass as floating drift are sea and ocean bottoms.

Most sediment deposition occurs during floods, which may also drown animals that are then buried and preserved. The great majority of preserved dinosaurs, however, died before a given flood. The bottoms and edges of bodies of water, whether streams, rivers, or lakes, are prime preservation locations. In some cases these watery locations lead to exquisite preservation, including soft tissues. Also good are floodplains, although nonburial before the next seasonal flood results in their degradation by feeding vertebrates and invertebrates and exposure. An extreme means of fossilization with near-perfect preservation is tree sap, but this can capture only small remains, or animal parts. Once burial occurs, the processes that preserve remains are complex and in many regards poorly understood. It is being realized, for instance, that bacterial activity is often important in preserving organic bodies. Depending on the circumstances, fossilization can be rapid or very slow, to the point that it never really occurs even after millions of years. The degree of fossilization therefore varies and tends to be more extensive the further back in time the animal was buried. The most extreme fossilization occurs when the original bone is completely replaced by groundwater-borne minerals. Some Australian dinosaur bones have, for instance, been opalized. Most dinosaur bones, however, retain the original calcium structure. The pores have been filled with minerals, converting the bones into rocks much heavier than the living bones. In some locations such as the Morrison Formation, bacterial activity encouraged the concentration of uranium in many bones—skeletons still below the surface can be detected by their radiation—leading to a radiation risk from stored bones. In other cases the environment surrounding dinosaur bones has been so stable that little alteration has occurred, leading to the partial retention of some soft tissues near the core of the bones.

While dinosaur bones are on the scarce side, their trackways are much more abundant, with a single individual being able to leave behind lots of prints. Prints are left in sediments sufficiently moist to record them, usually along the

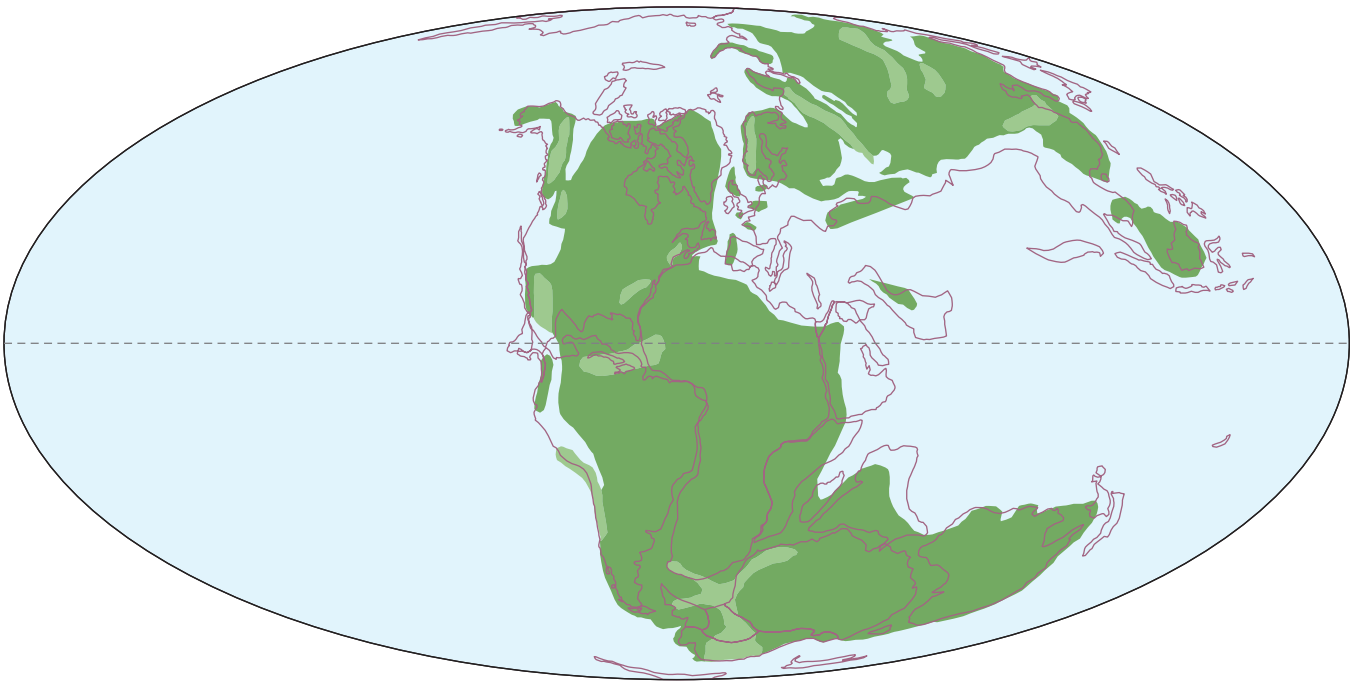
edges of water bodies such as streams, rivers, ponds, lakes, and ocean beaches. Sometimes they are stabilized by algal and bacterial mats that that keep them from eroding until the next influx of sediment preserves them. Or windblown sediments are the initial agent of preservation. Or the prints may be degraded, especially if made in soft mud that quickly slumped. Wet places are not necessary to retain prints, as some have been found on the flanks of fossil dunes. Most evocative are tracks associated with raindrop impressions from showers too brief to ruin the prints. Tracks are usually revealed by horizontal splitting of slabs, and in that case it is not always true that the print on view is the one directly impressed by the foot; if the print lacks foot pad scales, then the split layer may or may not be one above or below the surface stepped upon back in the Mesozoic. Sometimes prints are exposed in a vertical section as profiles. Generally, where trackways are common, bones are not, although this separation may be between levels in the same formation. Some places are dinosaur track freeways dense with trails, from little species and juveniles to giant adults; these are usually shoreline deposits patrolled by predatory dinosaurs and used as open traffic corridors. Trackways are often found as part of quarrying operations, where they may be studied before destruction, or removal for scientific or commercial purposes. Prints are the most common privately collected dinosaur fossils. As for other trace fossils, don't forget the poop that can be fairly abundant in some places—coprolites—and the polished gastroliths that may be present scattered in sediments that are otherwise barren of rocks. Eggs, often at least their broken shells, and nests are not extremely rare—having often been buried by the parents, their preservation is not all that surprising.

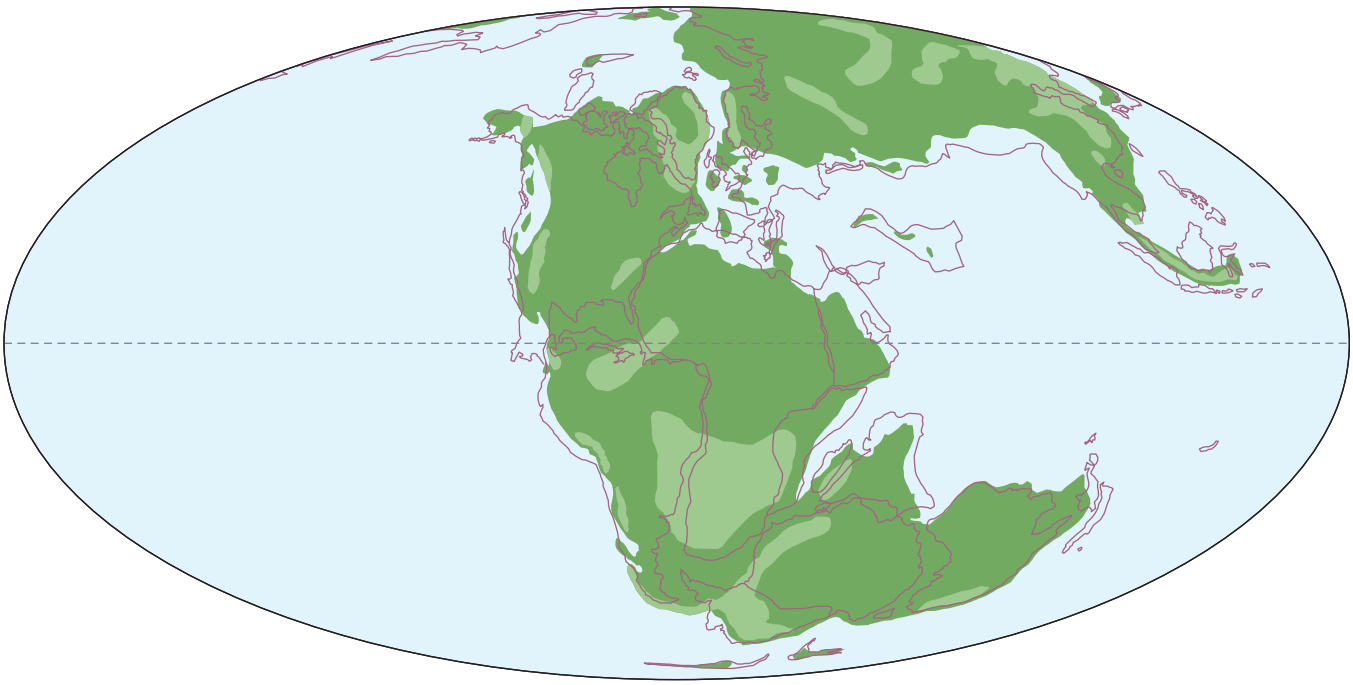
Although the number of dinosaur bones and trackways that lie in the ground is tremendous, all but a tiny fraction are for practical reasons out of reach. Nearly all are simply buried too deeply. The great majority of fossils that are found are on or within a few feet of the surface. Occasional exceptions include deep excavations such as construction sites and quarries, or mining operations. The famed *Iguanodon*s of Belgium were found in deep coal mines of the 1800s long since flooded. Even if deposits loaded with dinosaur fossils occur near the surface, their discovery is difficult if a heavy cover of well-watered vegetation and soil hides the sediments. For example, large tracts of dinosaur-bearing Mesozoic sediments lie on the Eastern Seaboard, running under major cities such as Washington, DC, and Baltimore. But the limited access to the sediments hinders discoveries, which are limited largely to construction sites made available by willing landowners. A dinosaur enthusiast, to the surprise of local professionals, recently found abundant prints as well as a squashed baby ankylosaur in suburban Maryland, most in creek beds. Coastal cliffs made up of Mesozoic deposits are another location for dinosaur hunting in forested areas, but they can be dangerous as they erode and collapse.

Prime dinosaur real estate consists of suitable Mesozoic sediments that have been exposed and eroded over large areas that are too arid to support heavy vegetation. This includes shortgrass prairies, badlands, and deserts. There are occasional locations in which dinosaur bone material is so abundant that their remains are easily found with little effort, especially before they have been picked over. Dinosaur Provincial Park in southern Alberta is a well-known example. In some locations countless trackways have been exposed. In most cases dinosaur bones are much less common. Finding dinosaurs has changed little since the 1800s. It normally consists of walking slowly, stooped over, usually under a baking sun, often afflicted by flying insects, looking for telltale traces. If really small remains are being looked for, such as fragmented eggshells, crawling on (padded) knees is necessary. Novices often miss the traces against the background of sediments, but even amateurs soon learn to mentally key in on the characteristics that distinguish fossil remains from rocks. Typically, broken pieces of bones on the surface indicate that a bone or skeleton is eroding out. One hopes that tracing the broken pieces upslope will soon lead to bones that are still in place. In recent years GPS has greatly aided in determining and mapping the position of fossils. Ground-penetrating radar has sometimes been used to better map out the extent of a newly found set of remains, but usually researchers just dig and see what turns up.

Now it becomes a matter of properly excavating and removing the fossil without damaging it while scientifically investigating and recording the nature of the surrounding sediments in order to recover the information they may contain. These basic methods have also not changed much over the years. On occasion thick overburden may be removed by heavy equipment or even explosives. But usually it is a job for jackhammers, sledgehammers, picks, or shovels, depending on the depth and hardness of the sediments and the equipment that can be brought in. When the remains to be recovered are reached, more-careful excavation tools, including trowels, hammers and chisels, picks, and even dental tools and brushes, are used. It is rare to be able to simply brush sand off a well-preserved fossil as in the movies, although this happy circumstance does occur in some ancient dune deposits in Mongolia. Usually sediments are cemented to some degree and require forceful action. At the same time, the bones and other remains are fragile, and care must be taken to avoid damaging them. And their position has to be documented by quarry maps, photography, or laser scanning before removal. Individual bones can be removed, or blocks of sediment including multiple bones or articulated skeletons may have to be taken out intact. Again, these operations are usually conducted under conditions that include flying insects, dust, heat, and sun, although tarps can provide shade. In Arctic locations heat is not a problem, but insect swarms are intense during the summer field season. The summer season has been abandoned in some locations because the melted sediments of river cliffs are a serious avalanche danger, so digs are conducted in the extreme Arctic cold.

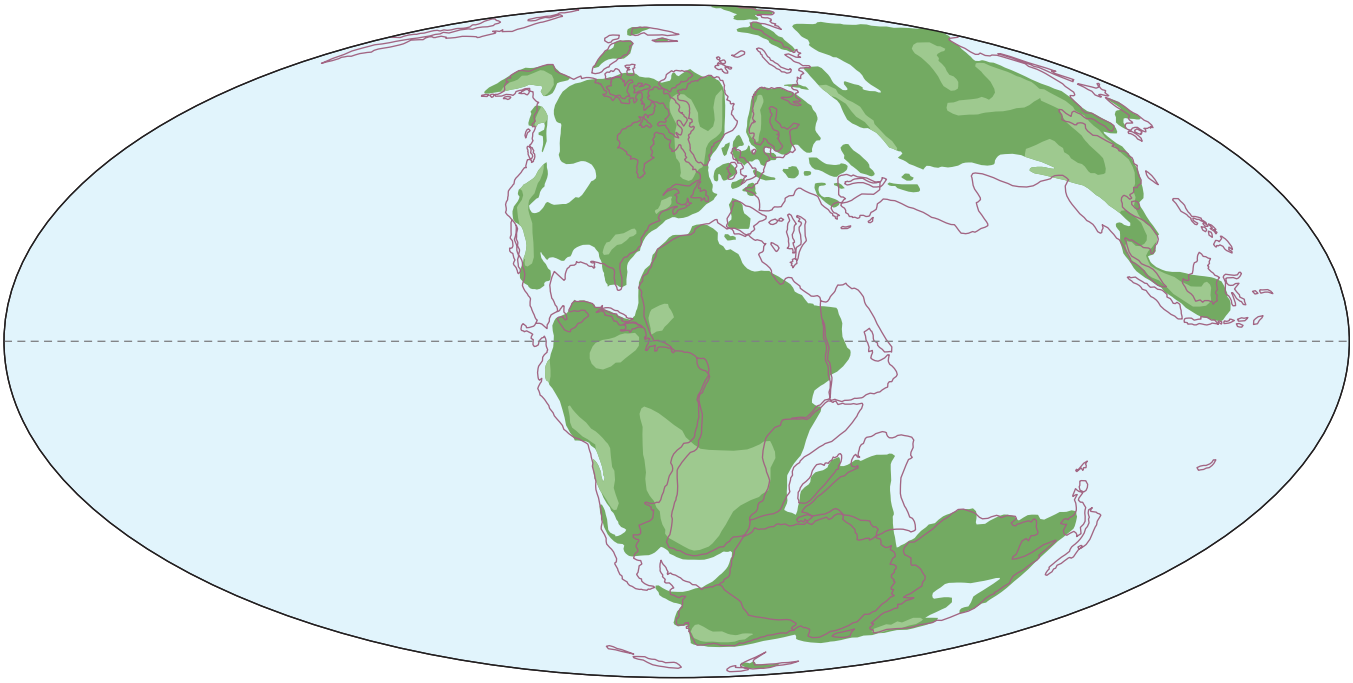
Late Triassic (Rhaetian–Norian–Carnian)

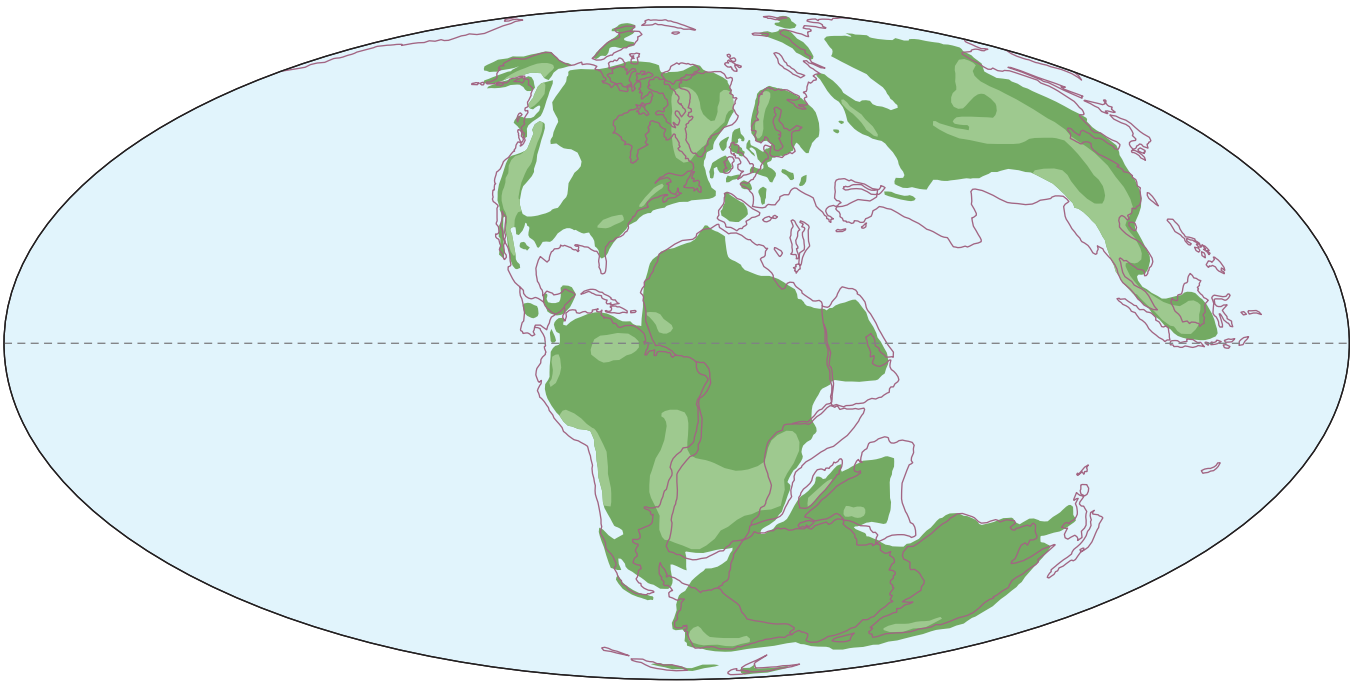




Early Jurassic (Sinemurian)

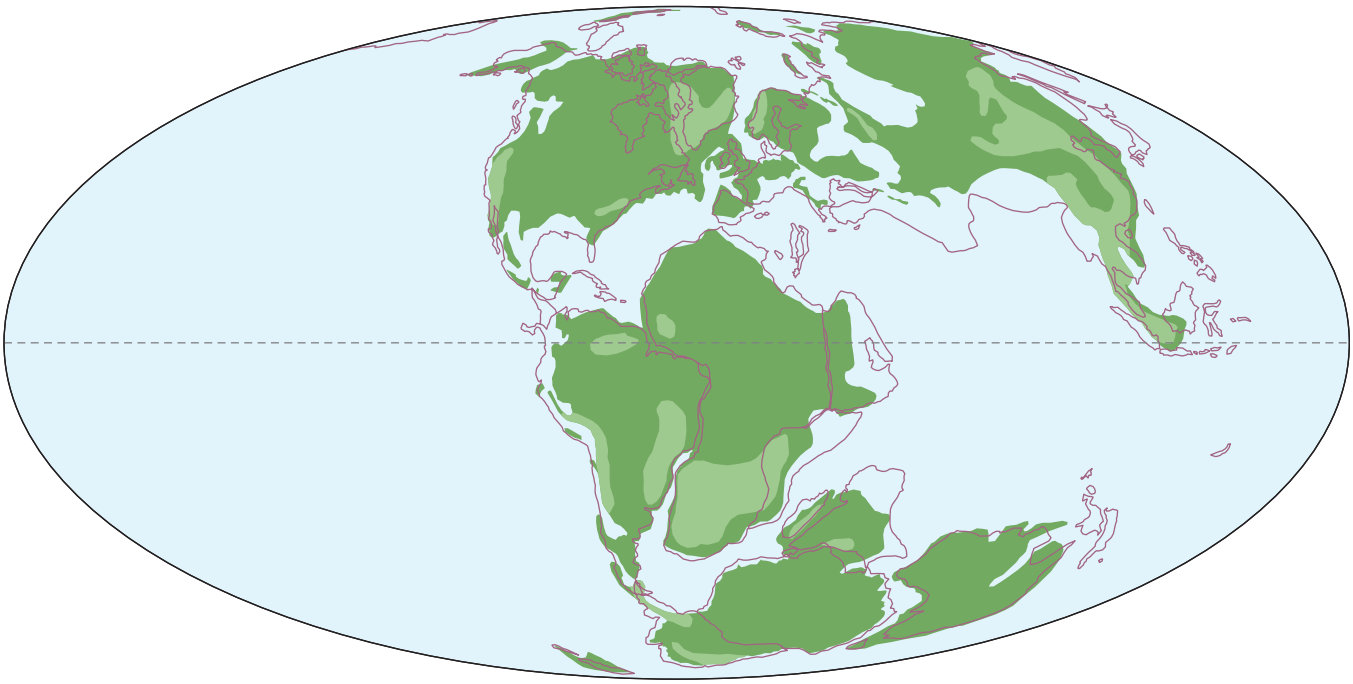
Middle Jurassic (Callovian)

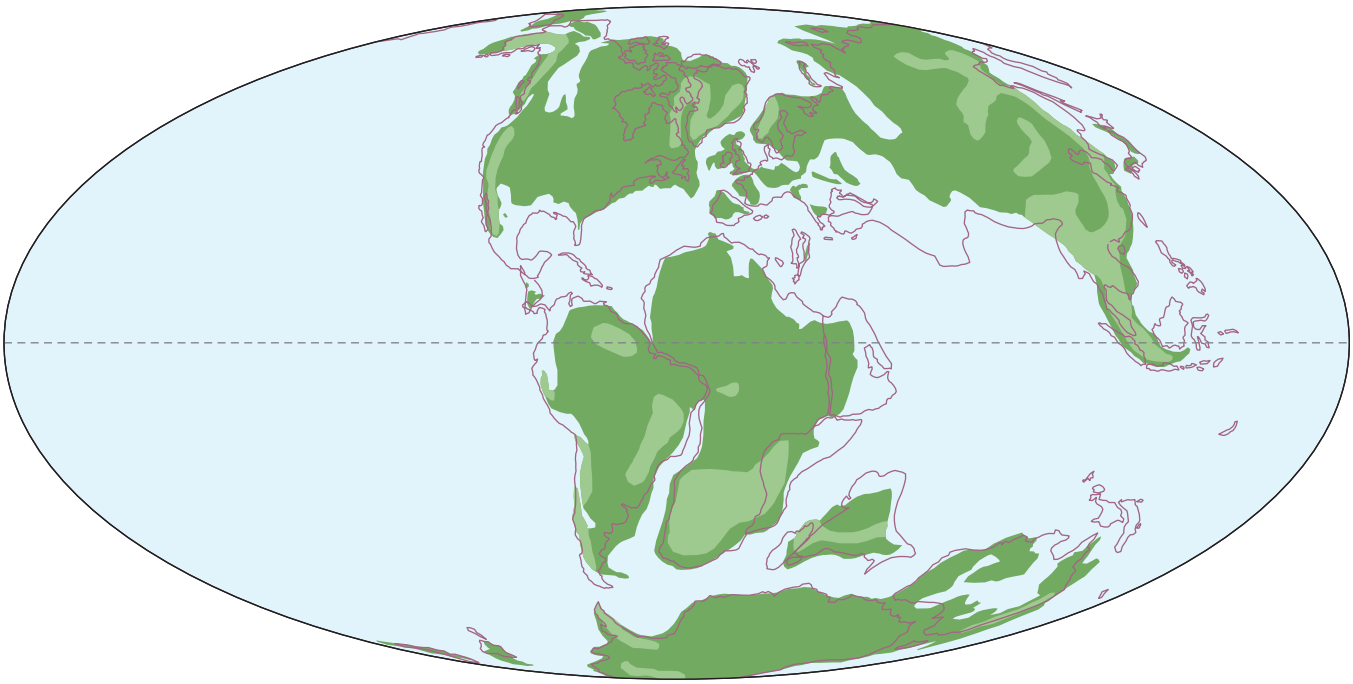




Late Jurassic (Kimmeridgian)

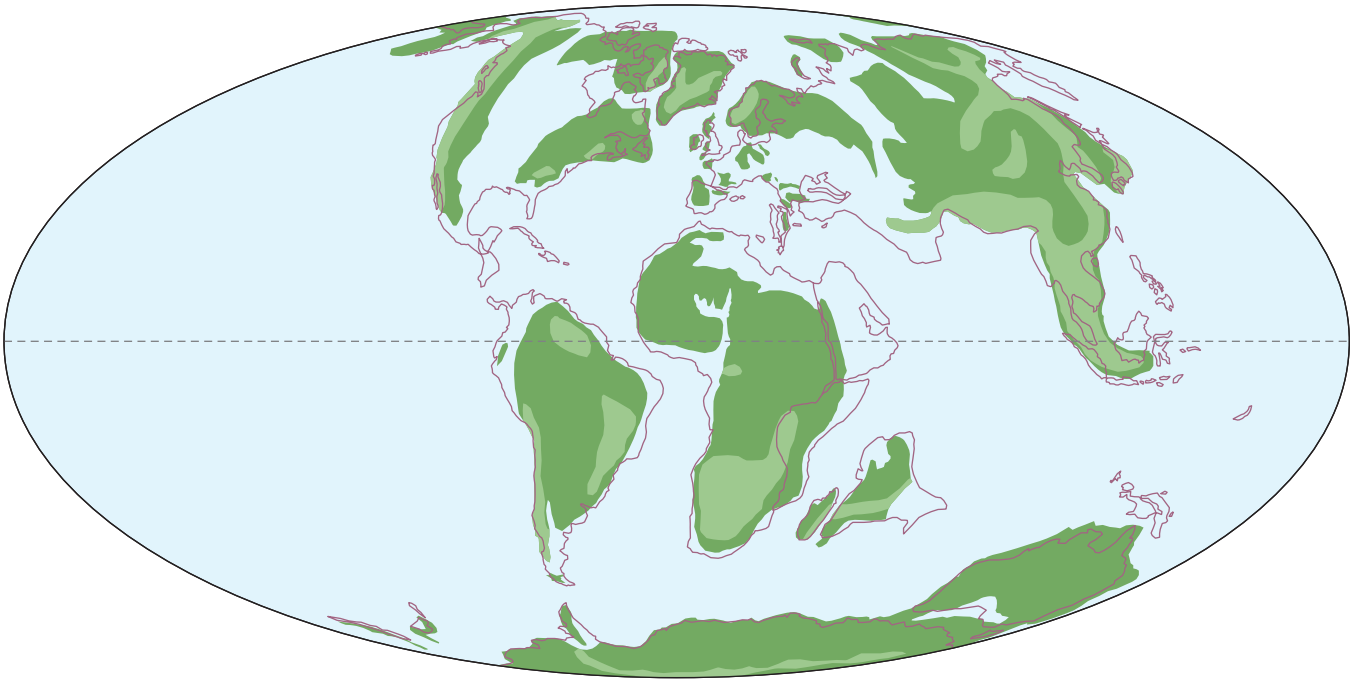
Early Cretaceous (Valanginian–Berriasian)

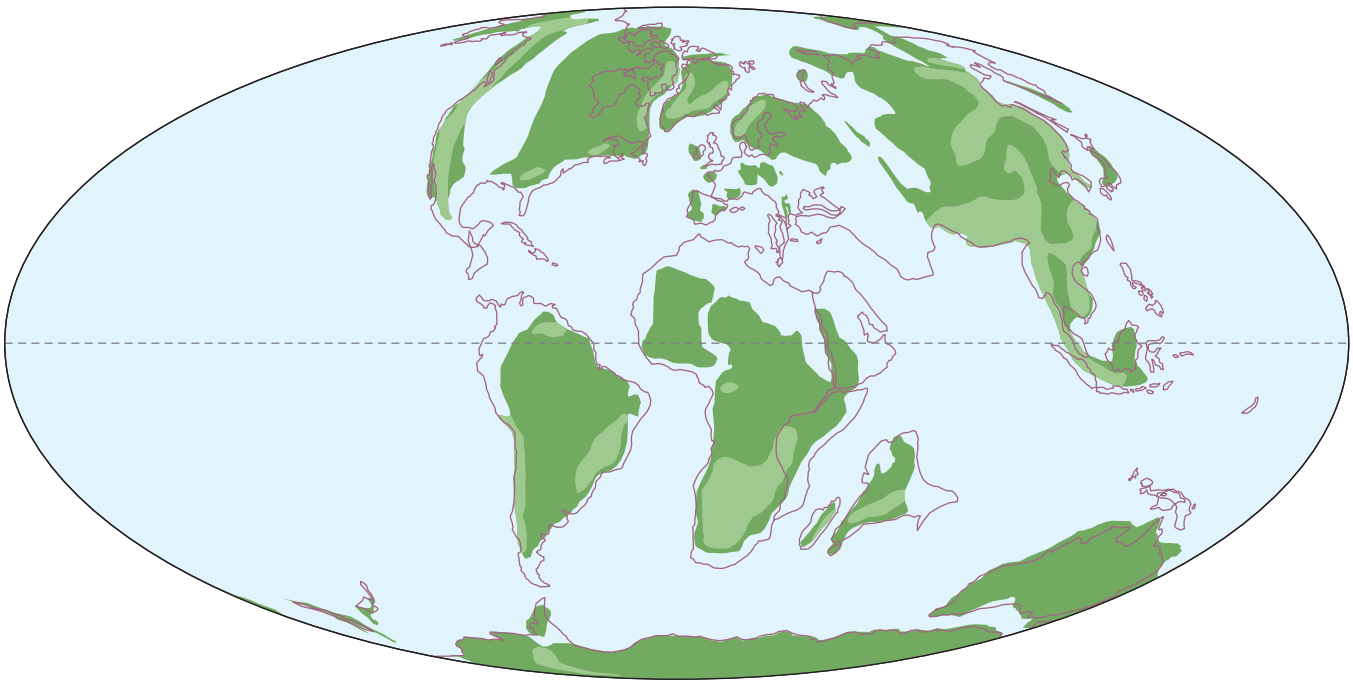




Early Cretaceous (Aptian)

Late Cretaceous (Coniacian)





Late Cretaceous (Campanian)

After exposure, especially fragile bones may be soaked with glue to harden them. On the other hand, the increasingly sophisticated techniques being applied to bones in the laboratory discourage alteration and contamination of bones. Before removal, most remains are quickly covered with tissue paper that is wetted in place, followed by heavier paper, and over that a thick layer of plaster to form a protective jacket. Wood is usually used to brace the jacket. When the top is so protected, the remains are undermined and then flipped—a process often requiring considerable exertion and entailing some risk to both excavators and the fossils. Then the other side is papered and plastered, forming a protective cocoon. These techniques have changed little in over a century. If the jacketed block is very heavy and not accessible to heavy equipment, a helicopter may be brought in to lift it out. On occasion this requires a heavy-lift helicopter; the US Army is sometimes willing to conduct such operations gratis as part of dissimilar cargo training that allows its crews to learn how to cope with challenging objects rather than standard pallets.

Because dinosaur paleontology is not a high-priority science backed by large financial budgets, and because the number of persons searching for and excavating dinosaurs in the world in a given year is only a few thousand—far more than in the past—the number of dinosaur skeletons that now reside in museums is still just a few thousand. A growing exception is China, where state funding is filling warehouses and new museums with material.

In the lab, preparators remove part or all of the jacket and use fine tools to eliminate some or all of the sediment from the bones and any other remains. Most bones are left intact, and only their surface form is documented. In some situations chemical treatment is required to stabilize bones; this is especially true if the bones are impregnated with pyrite, which gradually swells with moisture. Increasingly, certain bones are opened to reveal their internal structure for various purposes: sectioning is used to examine bone histology and microstructure, to count growth rings, to search for traces of soft tissues, and to sample bone isotopes and proteins. It is becoming the norm to conduct CT scans on skulls and complex bones as a means to determine the three-dimensional structure without invasive preparation, as well as to reduce costs. These can be published as conventional hard copies and in digital form. There is increasing reluctance to put original bones in mounted skeletons in display halls because delicate fossils are better conserved when properly curated in the back areas. And mounting heavy, fragile bones poses many difficulties and limitations while removing them from ready study. Instead, the bones are molded, and lightweight casts are used for the display skeleton.

There has never been as much dinosaur-related activity as there is today. At the same time, there is the usual shortage of funding and personnel compared to what could otherwise be done. The happy outcome is that there are plenty of opportunities for amateurs to participate in finding and preparing dinosaurs. If nonprofessionals search for fossils on their own, they need to pay attention to laws and to paleontological ethics. In some countries all dinosaur fossils are regulated by the state—this is true in Canada, for instance. In the United States, fossils found on privately held land are entirely the property of the landowner, who can dispose of any prehistoric remains as he or she sees fit. Any search for and retention of fossils on private property is therefore by permission of the owner, many but not all of whom are interested in the fossils on their land. Because dinosaur remains in the eastern states usually consist of teeth and other small items, nonhazardous construction sites are often available for exploration on nonwork days. In the West, ranches with cooperative owners are primary sources of dinosaur remains. The rising sums of money to be made by selling fossils are making it more difficult for scientific teams to access such lands. The religious opinions of some landowners are also an occasional barrier. Fortunately, dinosaur fossils are a part of western lore and heritage, so many locals favor paleontological activities, which contribute to the tourist trade. All fossils on federal government land are public property and are heavily regulated. Removal can occur only with official permission, which is limited to accredited researchers. Environmental concerns may be involved because dinosaur excavations are in effect small-scale mining operations. Fossils within Indian reservations may likewise be regulated, and collaboration with resident natives is indispensable. Dinosaur fossils found by nonprofessionals searching on their own should not be disturbed. Instead they should be reported to qualified experts, who can then properly document and handle the remains. In such cases the professionals are glad to do so with the assistance of the discoverer.

A number of museums and other institutions offer courses to the public on finding, excavating, and preparing dinosaurs and other fossils. Most expeditions include unpaid volunteers who are trained, often on-site, to provide hands-on assistance to the researchers. Participants are usually expected to pay for their own transportation and general expenses, although food and in some cases camping gear as well as equipment may be provided. In order to tap into the growing number of dinosaur enthusiasts, commercial operations led by qualified experts provide a dinosaur-hunting experience for a fee, usually in the western states and Canada. Those searching for and digging up dinosaurs need to take due precautions to protect themselves from sunlight and heat, in terms of UV exposure, dehydration, and hyperthermia, as well as biting and stinging insects and scorpions. Rattlesnakes are often common in the vicinity of dinosaur fossils. Steep slopes, cliffs, and hidden cavities are potential dangers. In many dinosaur formations gravel-like caliche deposits that formed in the ancient, semiarid soils create roller-bearing-like surfaces that undermine footing. Flash floods can hit quarries

or ill-placed campsites. The use of mechanical and handheld tools when excavating fossils poses risks, as does falling debris from quarry walls. When impact tools are used on hard rock, eye protection may be necessary. Chemicals used while working with fossils require proper handling.

Back in the museums and other facilities, volunteers can be found helping to prepare fossils for research and display, and cataloging and handling collections. This is important work because, in addition to the constant influx of new fossils with each year's harvest, many dinosaur fossils found as long as a century ago have been sitting on shelves, sometimes still in their original jackets, without being researched.

Landowners who allow researchers onto their land sometimes get a new species found on their property named after them, informally or formally. So do volunteers who find new dinosaurs. Who knows, you may be the next lucky amateur.

USING THE GROUP AND SPECIES DESCRIPTIONS

About 1,700 dinosaur species have been named, but a large portion of these names are invalid. Many are based on inadequate remains, such as teeth or one or a few bones, that are taxonomically indeterminate. Others are junior synonyms for species that have already been named. *Dynamosaurus*, for instance, proved to be the same as the previously named *Tyrannosaurus*, which had been named shortly before, so the former is no longer used. This guide includes mainly those species that are generally considered valid and are based on sufficient remains. A few exceptions are allowed when a species based on a single bone or little more is important in indicating the existence of a distinctive type or group of dinosaurs in a certain time and place. Many of the group and species entries have been changed very little if at all from the first and/or second editions; corrections and new information have caused a substantial minority to be more heavily revised, and in a few cases dropped, at the same time that a large array of new species have been added.

The species descriptions are listed hierarchically, starting with major groups and working down the ranking levels to genera and species. Because many researchers have abandoned the traditional Linnaean system of classes, orders, suborders, and families, there is no longer a standard arrangement for the dinosaurs—many dinosaur genera are no longer placed in official families—so none is used here. In general the taxa are arranged phylogenetically. This presents a number of problems. It is more difficult for the general reader to follow the various groupings. Although there is considerable consensus concerning the broader relationships of the major groups, at lower levels the incompleteness of the fossil record hinders a better understanding. The great majority of dinosaur species are not known, many of those that are known are documented by incomplete remains, and it is not possible to examine dinosaur relationships with genetic analysis. Because different cladistic analyses often differ substantially from one another, I have used a degree of personal choice and judgment to arrange the groups and species within the groups. Some of these placements reflect my considered opinion, while others are arbitrary choices between competing research results. Most of the phylogeny and taxonomy offered here is not a formal proposal, but a few new group labels were found necessary and are coined and defined here for future use by others if it proves efficacious. Disputes and alternatives concerning the placement of dinosaur groups and species are often but not always mentioned.

Under the listing for each dinosaur group, the overall geographic distribution and geological time span of its members are noted. This is followed by the anatomical characteristics that apply to the group in general, which are not repeated for each species in the group. The anatomical features usually center on what is recorded in the bones, but other body parts are covered when they have been preserved. The anatomical details are for purposes of general characterization and identification and reflect as much as possible what a dinosaur watcher might use; they are not technical phylogenetic diagnoses. The type of habitat that the group favored is briefly listed, and this varies from specific in some types to very generalized in others. Also outlined are the restored habits that probably characterize the group as a whole. The reliability of these conclusions varies greatly. There is, for example, no doubt that theropods with bladed, serrated teeth consumed flesh rather than plants. There is also little doubt that the sickle-clawed *Velociraptor* regularly attacked the similar-sized herbivore *Protoceratops*—there is even an example of two skeletons still locked in combat. Less certain is exactly how *Velociraptor* used its sickle claws to dispatch prey on a regular basis. It is not known whether *Velociraptor* packs attacked the much larger armored *Pinacosaurus* that lived in the same desert habitat. Some dinosaurs are head-scratchers to varying degrees as far as their habits.

The naming of dinosaur genera and species is often problematic, in part because of a lack of consistency. In some cases genera are badly oversplit. For example, almost every species of tyrannosaurid receives a generic title despite the high uniformity of the group. A similar situation is true of chasmosaurine and centrosaurine ceratopsids, and of kritosaur and hypacrosaur hadrosaurs, in which the core skulls and skeletons are often very similar; the characters that vary are the crests, frills, and horns used for species-level identification. A number of species are probably one of the growth stages of another species. Meanwhile, a large number of species have been appropriately placed in the

genus *Psittacosaurus*, and iguanodont species have tended to be placed in too few genera and species. The inconsistency in naming genera is seen when comparing the great variation between *Psittacosaurus gobiensis* and *P. sibiricus* versus the very close similarity of *Corythosaurus* and *Lambeosaurus*. Among sauropods it has been recognized that the apatosaurs were overlumped, resulting in the revival of *Brontosaurus*. In this work I have attempted to apply more uniform standards to generic and species designations, with the divergences from the conclusions of others noted.

Also a big problem is the inadequate nature of the fossils that many dinosaur taxa are based on. Such is true of the original fossils of *Megalosaurus*, *Iguanodon*, *Allosaurus*, *Apatosaurus*, *Diplodocus*, *Stegosaurus*, *Stegoceras*, *Ornithomimus*, *Struthiomimus*, *Coelophysis*, *Spinosaurus*, *Brachiosaurus*, *Plateosaurus*, *Argentinosaurus*, *Alamosaurus*, *Troodon*, *Stenonychosaurus*, *Leaellynasaura*, and for that matter *Archaeopteryx*, the latter starting out as an isolated feather. Appeals to the International Commission on Zoological Nomenclature are helping. But sorting out species, genera, and families is often seriously hindered; these items are noted.

The entry for each species first cites the dimensions and estimated mass of the taxon. The total length is for the combined skull and skeleton along the line of the vertebrae; any tail feathers that further lengthened the dinosaur are not included. The values are general figures for the size of the largest known adults of the species and do not necessarily apply to the values estimated for specific fossils, most of which can be found via https://press.princeton.edu/books/hardcover/9780691231570/the-princeton-field-guide-to-dinosaurs-third-edition, including the mass estimates for each fossil. Because the number of fossils for a particular species is a small fraction of those that lived, the largest individuals are not measured; "world record" fossils can be a third or more heavier than is typical—recent estimates that the largest theropod species got to be two-thirds larger are improbable. The sizes of species known only from immature fossils are not estimated. All values are, of course, approximate, and their quality varies depending on the completeness of the remains for a given species. If the species is known from sufficiently complete remains, the dimensions and mass are based on the skeletal restoration. The latter is used to estimate the volume of the dinosaur, which can then be used to calculate the mass, with the portion of the volume that was occupied by lungs and any air sacs taken into account. It has been realized of late that animals are generally denser than had been thought. Most land mammals when swimming, for example, are nearly awash and avoiding drowning only by swimming, so the density, or specific gravity (SG), is set at 1 relative to the density of water for most dinosaurs lacking air sacs. Armored dinosaurs were likely significantly denser than water, so their SGs were 1.06 to 1.1. Flying birds with very highly pneumatic skeletons can have low densities, but such values are not applicable to dinosaurs with air sacs because their limb bones are not so air filled, including the early winged forms. The big ratites whose leg bones are hollow float a little higher in water than mammals, suggesting SGs of 0.92. Because pneumatic theropods and sauropods lacked airy leg bones, their SG was probably between that and 0.96, with large examples being denser. A complication with sauropods is that their necks would have been less dense than the rest of the animal, and neck volume varied a lot relative the latter; modeling indicates the SG of their necks was 0.85 to 0.9, calculated separately. When remains are too incomplete to directly estimate dimensions and mass, these are extrapolated from those of relatives and are considerably more approximate. Both metric and English measurements are included except for metric tonnes, which equal 1.1 English tons; all original calculations are metric, but because they are often imprecise, the conversions from metric to English are often rounded off as well.

The next line outlines the fossil remains, whether they are skull or skeletal material or both, that can be confidently assigned to the species to date; the number of fossils varies from one to thousands. The accuracy of the list ranges from exact to a generalization. The latter sometimes results from recent reassignment of fossils from one species to another, leaving the precise inventory uncertain. Skeletal and/or skull restorations have been rendered for those species that are known from sufficiently complete remains that have been adequately documented by the time the book was being finalized to execute a reconstruction—or for species that are of such interest that a seriously incomplete restoration is justified (the rather poorly known but oversized new oviraptorosaur *Gigantoraptor* being an example, as is the long-known but still very incomplete *Ankylosaurus*). A number of species known from good remains have yet to be made available for research, sometimes decades after their discovery. In some cases only oblique-view photographs unsuitable for a restoration of reasonably complete skulls and skeletons are obtainable. The pace of discovery is so fast that a few new finds could not be included. A few complete skeletons are so damaged or distorted that a restoration is not feasible; this is true of the flattened Yixian *Psittacosaurus* with skin impression and bristles, and *Chasmosaurus irvinensis*. Only when at least some skull material is on hand is a skeletal included, the exception being a number of the small-headed sauropods, stegosaurs, and therizinosaurs, as skulls are scarce in those groups. When enough examples of some major dinosaur types are not sufficient, the remains of multiple species have been used to construct a composite representation, such as for the derived alvarezsaurid and therizinosaurid. Despite the absences, this is by far the most extensive Mesozoic dinosaur skull-skeletal library yet published in print. The core skeletal fossils that have been restored can be found at the above link. The restorations show the bones as solid white set within the solid black restored muscle and keratin profiles; cartilage is not included. Absence of most or all of the skull often precludes a restoration, those

dinosaurs with small skulls being the most common exception. In many cases only the skull is complete enough for illustration. When more than one skeleton and/or skull of a given species is included, they are always to the same scale to facilitate size comparisons. In most cases the skull and skeletal restorations are of adults or close to it, but growth series are included for all examples that are achievable, on the premise that young dinosaurs soon left their nests and were part of the general fauna. In some examples the skeletons of the smallest juveniles are reproduced both to scale to the much larger adults, and at a larger scale to allow details to be better seen—this guide contains the largest set to date of dinosaur growth stages. The accuracy of the restorations ranges from very good for those that are known from extensive remains that have been described in detail and/or for which good photographs are on hand, down to approximate if much of the species remains are missing or have not been well illustrated. The restorations have been prepared over four decades to fulfill differing requirements. A number of skeletons and skulls show only those bones that are known—sometimes with replications of one side to the other, ranging from a large fraction to nearly all—whereas others have been filled out to represent a complete skeleton. Reliable information about exactly which bones have and have not been preserved is often not available, so the widely used term "rigorous restoration" of incomplete skeletals is best avoided in favor of "known bone." Top views of skeletons have been provided when such were doable, but in many cases lateral crushing prevented that. The skeletons are posed in a common basic posture, with the right hind leg pushing off at the end of its propulsive stroke, in order to facilitate cross comparisons. Representative examples of shaded skull restorations have been included with some of the major groups. The same has been done with a sample of muscle studies, whose detailed nature is no less or more realistic than are the particulars in the full-life restorations, which, if anything, involve additional layers of speculation.

The color plates are based on species for which the fully or nearly adult skeletal restorations or skulls are deemed of sufficient quality for a full-life restoration. If it is unlikely that new information will significantly alter the skeletal plan in the near future, a life restoration has been prepared; if the skeletal is not sufficiently reliable, a life restoration has not been done. A few of the earlier life restorations have been replaced because of updates of their skeletal restorations. Most of the skull as well as the skeleton needs to be present to justify a life restoration of an entire animal—although *Majungasaurus* bones are exquisitely preserved, there are too many uncertainties about its unusual proportions to warrant a life drawing. In a few cases color restorations were executed, despite significant questions about the skeletal study, because the species is particularly important or interesting for one reason or another, the spectacularly feathered but incomplete *Beipiaosaurus* being an example. In a few cases only the skull is good enough to warrant a life restoration to the exclusion of the overall body. The colors and patterns are entirely speculative except in the few cases where feather coloration has been restored—there is no consistent effort to coordinate speculative color patterns for a species between the life profiles and full-color scenes. Extremely vibrant color patterns have generally not been used to avoid giving the impression that they are identifying features. Those who wish to use the skeletal, muscle, and life restorations herein as the basis for commercial and other public projects are reminded to first contact the copyright illustrator.

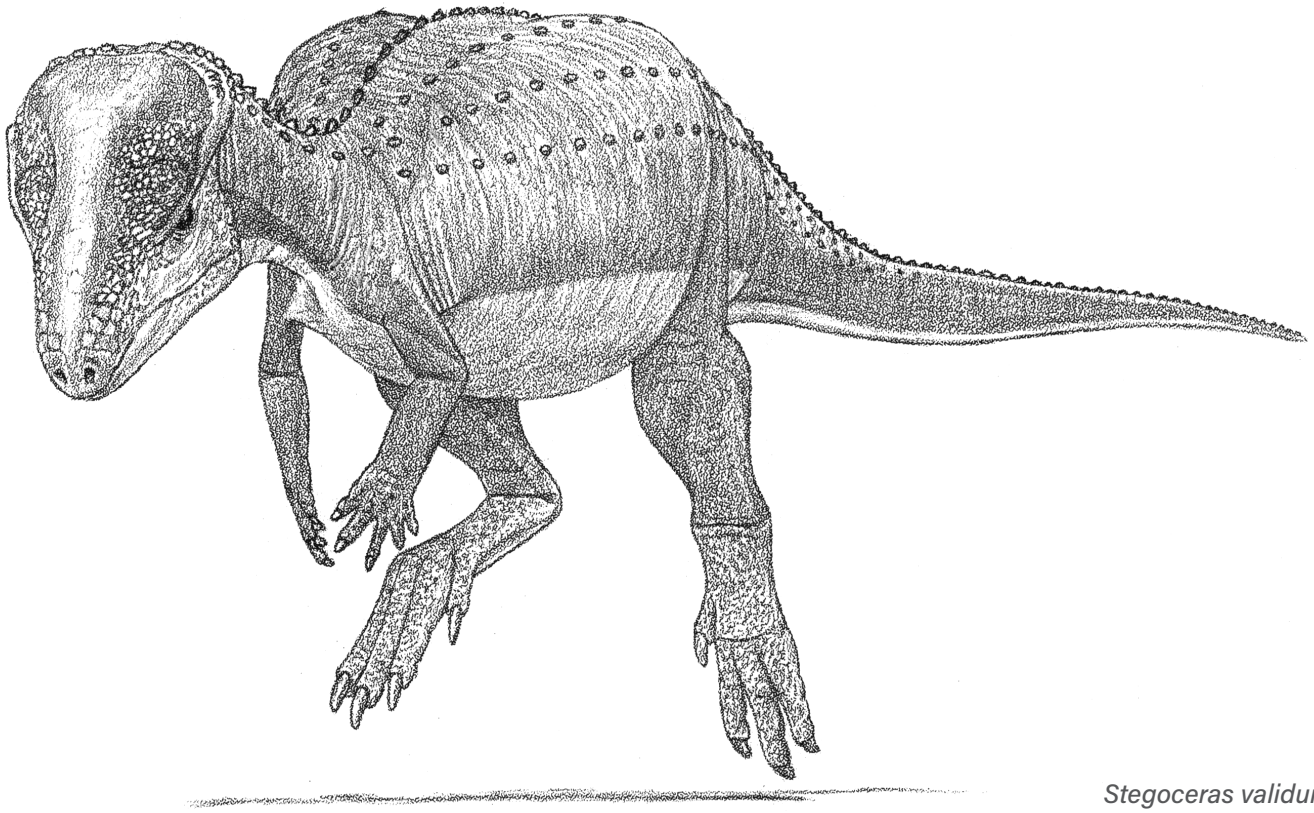
The particular anatomical characteristics that distinguish the species are listed, but these too are for purposes of general identification by putative dinosaur watchers, not for technical species diagnoses. These differ in extent depending on the degree of uniformity versus diversity in a given group as well as the completeness of the available fossil remains. In some cases the features of the species are not different enough from those of the group to warrant additional description. In other cases not enough is known to make a separate description possible.

Listed next is the formal geological time period and, when available, the specific stage that the species is known from, and the segment of that stage from early to middle to late. As discussed earlier, the age of a given species is known with a precision of within a million years in some cases, or as poorly as an entire period in others. The reader can refer to the time scale on the timeline chart to determine the age, or age range, of the species in years (see pp. 80–81). Because most species exist for only a few hundred thousand years before either being replaced by a descendant species or going entirely extinct, when fossils within a single genus are found in sediments that span more than that amount of time it is presumed they are different species. In some cases it is not entirely clear whether a species was present in just one time stage or crossed the boundary into the next one. In those cases the listing includes "and/or," such as late Santonian and/or early Campanian.

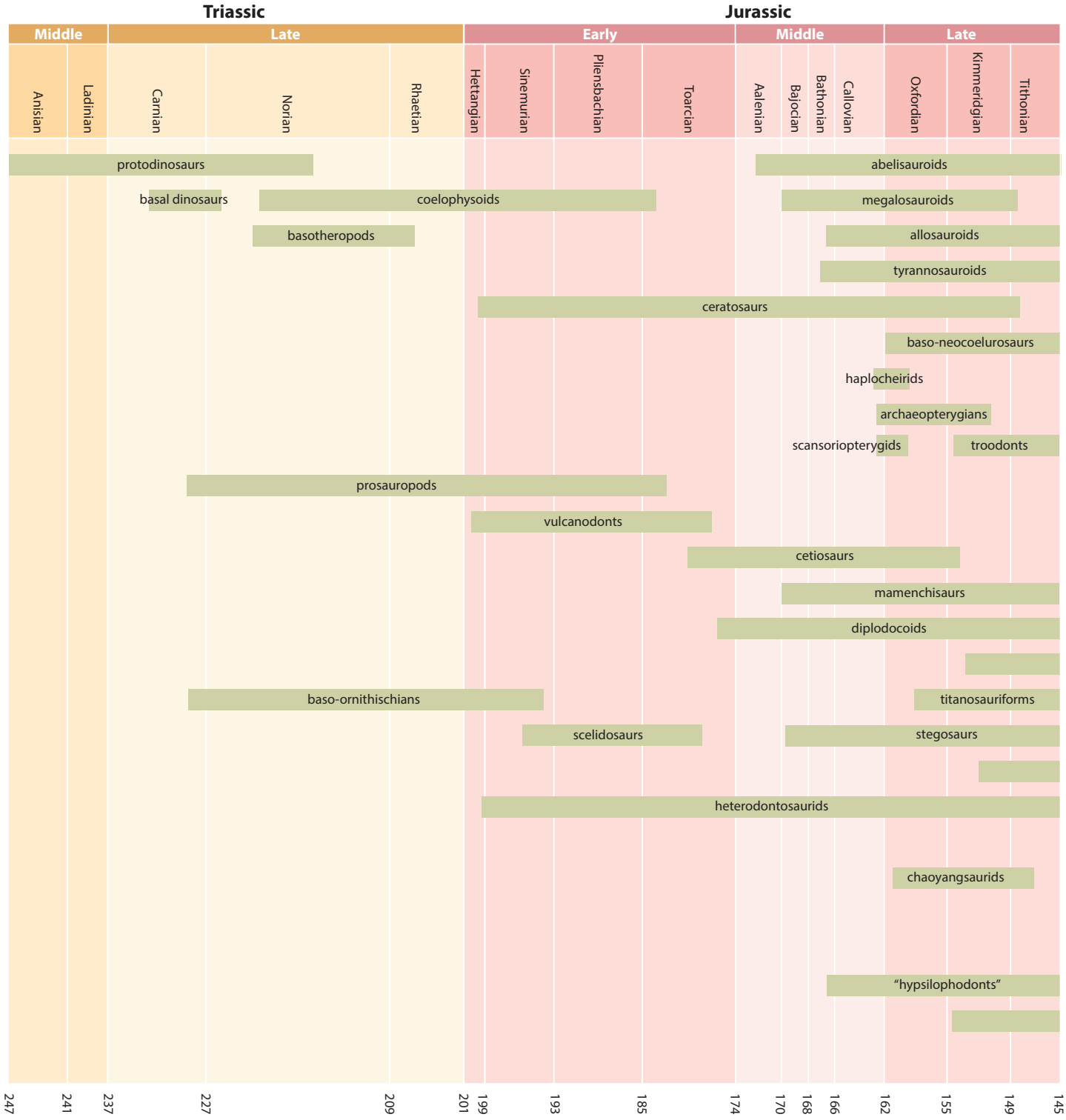
Next the geographic location and geological formation that the species is so far known from are listed. The paleomaps of coastlines (see pp. 71–74) can be used to geographically place a species in a world of drifting continents and fast-shifting seaways, with the proviso that no set of maps is extensive enough to show the exact configuration of the ancient lands when each species was extant. Some dinosaur species are known from only a single location and formation, whereas others have been found in an area spread over one or more formations. In the latter situation the first location/formation listed is for the original fossil. I have tended to be conservative in listing the presence of a specific species only in those places and levels where sufficiently complete remains are present. Some formations have not been named, even in areas that are well studied. Many formations were formed over a time span that was longer than that of some or all of the species that lived within them, so when possible the common procedure of

simply listing just the overall formation a given species is from is avoided. For example, a host of large herbivorous dinosaurs are often thought to have lived at the same time in the famous Dinosaur Park Formation in Alberta, including *Centrosaurus apertus*, *Styracosaurus albertensis*, *Chasmosaurus belli*, *Hypacrosaurus casuarius*, *Lambeosaurus lambei*, and *Parasaurolophus walkeri*. The actual situation over the million and a half years the formation was laid down is more complicated. In the lower, earlier portion of the formation dwelled *Centrosaurus apertus*, *Chasmosaurus russelli*, *Hypacrosaurus intermedius*, and the uncommon *Parasaurolophus walkeri*. In the middle of the formation dwelled *Centrosaurus apertus*, *Chasmosaurus belli*, *Hypacrosaurus intermedius*, and *Hypacrosaurus clavinitialis*. The upper or later sections of Dinosaur Park held the species *Styracosaurus albertensis*, *Chasmosaurus irvinensis*, *Hypacrosaurus intermedius*, *Hypacrosaurus lambei*, and later *Hypacrosaurus magnicristatus*. It has been assumed that one species of *Triceratops* and *Tyrannosaurus* lived during the ~1.5 million years it took to deposit the Hell Creek, Lance, and other formations, but the evidence favors species evolution in both over this period. Because the Morrison Formation was deposited over a span of six million years in the Late Jurassic, there was extensive change over time in the allosaurs, apatosaurs, diplodocines, camarasaurs, and stegosaurs that dwelled in the area. Many of the familiar particular species such as *Allosaurus fragilis*, *Camarasaurus lentus*, *Camptosaurus dispar*, and *Ceratosaurus nasicornis* are known from the middle of the formation, and later species of these genera are known from higher parts of the Morrison. Because the overlying Cedar Mountain Formation formed over 40 million years—suggesting a need to split the formation into smaller units—the fauna underwent radical changes. I have therefore listed the level of the formation that each species comes from, when this information is available. The reader can get an impression of what dinosaur species constituted a given fauna in a particular bed of sediments by using the formation index. Only species present at a given level of a formation could have lived together, but this does not always mean that a given set of dinosaurs listed as being from a particular level did so, because time separations sometimes exist. In a few cases the sediments a dinosaur is from are not yet named—often but not always because they have not been studied—and the geological group may be named instead, if one is available.

Noted next are the basic characteristics of the dinosaur's habitat in terms of rainfall and vegetation, as well as temperature when it is not generally tropical or subtropical year-round. Environmental information ranges from well studied in heavily researched formations to nonexistent in others. If the habits of the species are thought to include attributes not seen in the group as a whole, then they are outlined. Listed last are special notes about the species when they are called for. Possible ancestor-descendant relationships with close older or younger relatives are sometimes noted, but these are always tentative. This section is also used to note alternative hypotheses and controversies that apply to the groups and species.



Stegoceras validum


Triassic
Jurassic
Middle
Late
Early
Middle
Late
Anisian
Ladinian
Carnian
Norian
Rhaetian
Hettangian
Sinemurian
Pliensbachian
Toarcian
Aalenian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithonian
protodinosaurs
basal dinosaurs
coelophysoids
basotheropods
abelisauroids
megalosauroids
allosauroids
tyrannosauroids
ceratosaurs
baso-neocoelurosaurs
haplocheirids
archaeopterygians
scansoriopterygids
troodonts
prosauropods
vulcanodonts
cetiosaurs
mamenchisaurs
diplodocoids
baso-ornithischians
titanosauriformes
scelidosaurs
stegosaurs
heterodontosaurids
chaoyangsaurids
“hypsilophodonts”
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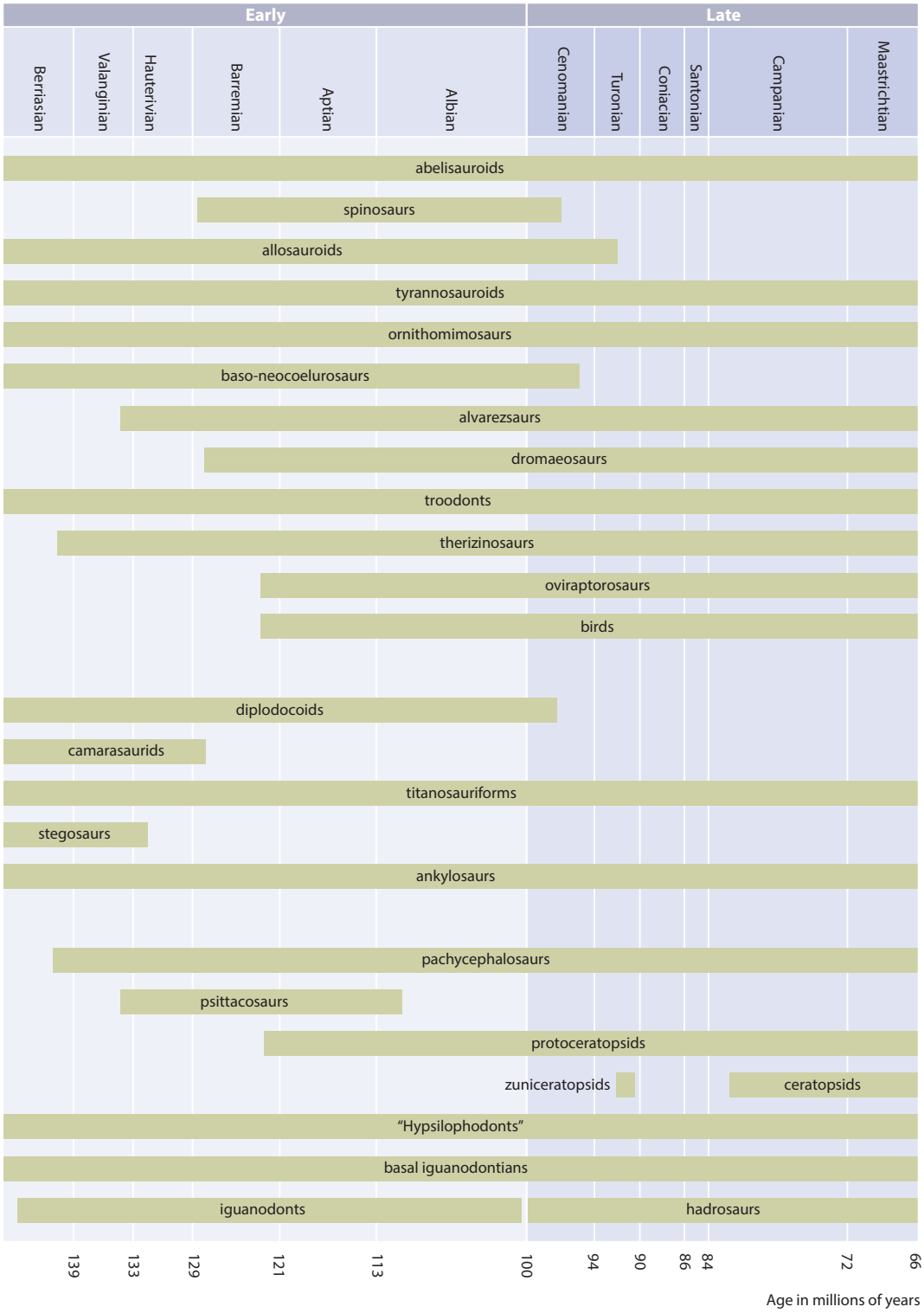
145

Cretaceous


Early
Late
Berriasian
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Santonian
Campanian
Maastrichtian
abelisauroids
spinosaurs
allosauroids
tyrannosauroids
ornithomimosaurs
baso-neocoelurosaurs
alvarezsaurs
dromaeosaurs
troodonts
therizinosaurs
oviraptorosaurs
birds
diplodocoids
camarasaurids
titanosauriforms
stegosaurs
ankylosaurs
pachycephalosaurs
psittacosaurs
protoceratopsids
zuniceratopsids
ceratopsids
"Hypsilophodonts"
basal iguanodontians
iguanodonts
hadrosaurs
139
133
129
121
113
100
94
90
86
84
72
66
Age in millions of years

Herrerasaurus ischigualastensis

DINOSAURS

SMALL TO GIGANTIC ARCHOSAURS FROM THE LATE TRIASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Diverse. Dorsal columns not highly flexible. Usually erect leg posture achieved by cylindrical femoral head fitting into a perforated hip socket and a simple hinge-jointed ankle, a few with more sprawling legs. All are hind-limb dominant in that legs are sole locomotory organs in walking and running and/or are more strongly built than the arms even when long-armed quadrupeds. Hands and feet digitigrade with wrist and ankle held clear of ground. Trackways show that when quadrupedal, hands always at least as far apart from midline as feet or farther; never hopped, and tail almost always held clear of ground. Body scales, when known and present, usually form a nonoverlapping mosaic pattern.

ENERGETICS Thermophysiology intermediate to very high energy.

REPRODUCTION AND ONTOGENY Usually reached sexual maturity while still growing, most were rapid breeders, many laid hard-shelled eggs in pairs, others may have laid soft-shelled eggs, growth rates moderate to rapid.

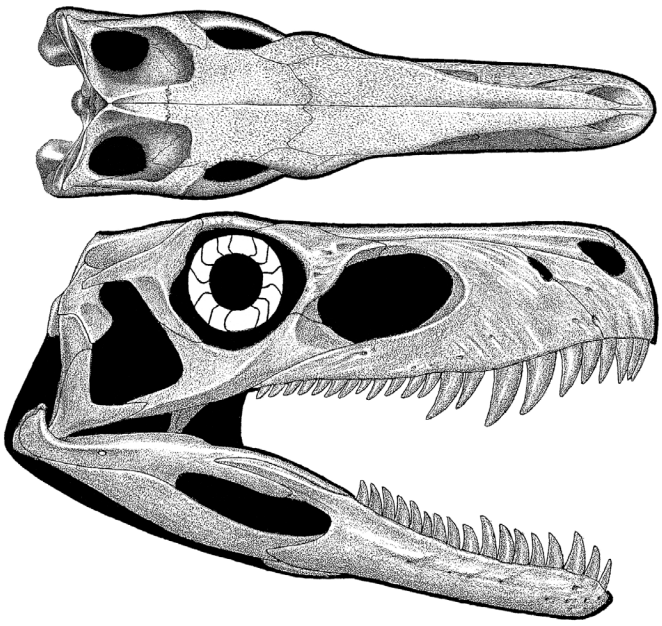
HABITATS AND HABITS Usually strongly terrestrial, although almost all able to swim, some able to fly. Predatory to herbivorous. Otherwise highly variable.

BASAL DINOSAURS

SMALL TO MODERATELY LARGE PREDATORY AND OMNIVOROUS DINOSAURS, LIMITED TO THE LATE TRIASSIC OF THE SOUTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly uniform. Generally lightly built. Heads moderately large, usually long and shallow, subrectangular, fairly narrow, fairly robustly constructed, skull bones usually somewhat loosely attached to one another, teeth usually serrated blades, sometimes not serrated and more leaf shaped. Necks moderately long, only gently S-curved. Tails long. Arms and four-fingered hands moderately long, claws well developed. Pelves short but deep, pubes procumbent to a little retroverted. Four load-bearing toes. Beginnings of birdlike respiratory system possibly present. Brains reptilian.

ENERGETICS Thermophysiology probably moderate, energy levels and food consumption probably lower than in most or all more derived predatory dinosaurs.



Herrerasaurus shaded skull

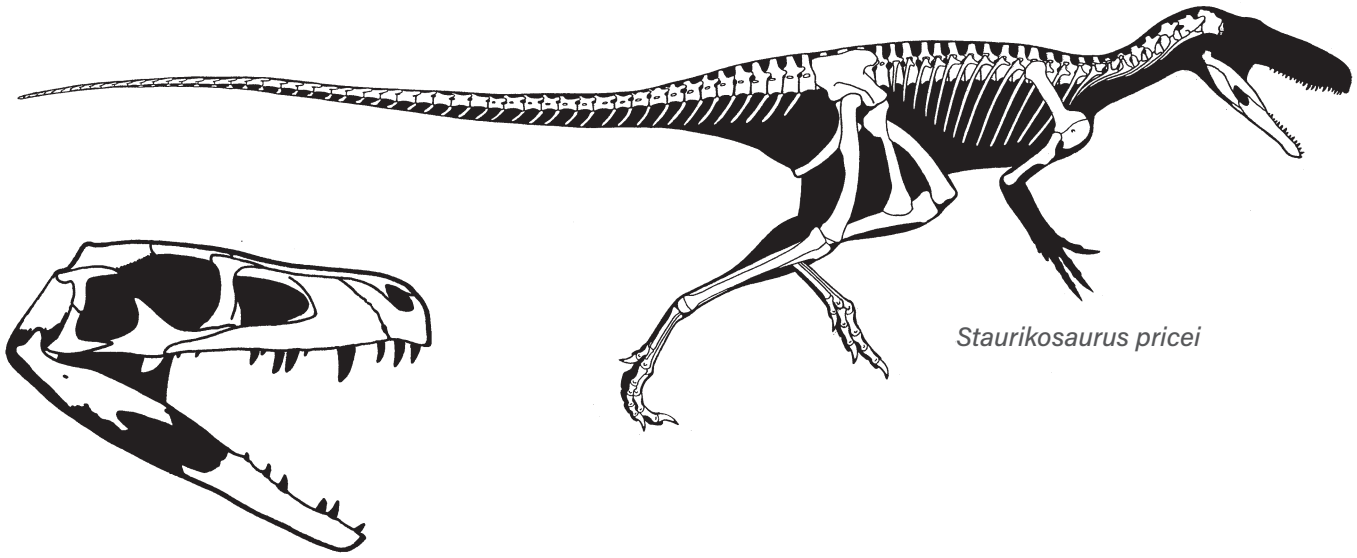
HABITS Pursuit predators, some also omnivorous. Head and arms primary weapons. Jaws and teeth delivered slashing wounds to disable muscles and cause bleeding, shock, and infection. Arms used to hold on to and control prey, possibly delivered slashing wounds. Adept surface swimmers, so able to cross large bodies of water, may have had some diving ability.
NOTES The most basal dinosaurs, their similarly generalized forms make it difficult to determine relationships with one another and major dinosaur groups, having variously been considered basal theropods, sauropodomorphs, saurischians, ornithoscelids, and paxdinosaurs. These briefly existing early dinosaurs were apparently not able to compete with more sophisticated examples. Fragmentary *Chindesaurus bryansmalli* and probably synonymous *Caseosaurus crosbyensis* indicate presence of cohort in southwestern United States; absence from at least some other continents probably reflects lack of sufficient sampling.

Alwalkeria maleriensis
— 1.5 m (5 ft) TL, 4 kg (8 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Back teeth bladed, front teeth less so, no teeth serrated.
AGE Late Triassic, Carnian.
DISTRIBUTION AND FORMATION/S Southeastern India; lower Maleri.
HABITS Probably omnivorous, hunted smaller game and consumed some easily digested plant material.
NOTES Possible close relative of *Eoraptor*, has been considered a very basal saurischian or theropod.

Sanjuansaurus gordilloi
— 3 m (9 ft) TL, 35 kg (80 lb)
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Teeth bladed and serrated. Pubis procumbent.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Northern Argentina; lower Ischigualasto.
HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.
NOTES Probable herrerasaur, has been considered a very basal saurischian, paxdinosaur, or theropod.

Staurikosaurus pricei
— 2.1 m (7 ft) TL, 13 kg (28 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Pubis nearly vertical.
AGE Late Triassic, middle Carnian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; upper Santa Maria.
NOTES Probable herrerasaur, has been considered a very basal saurischian, paxdinosaur, or theropod. Along with *Herrerasaurus cabreirai* may be earliest known dinosaurs.

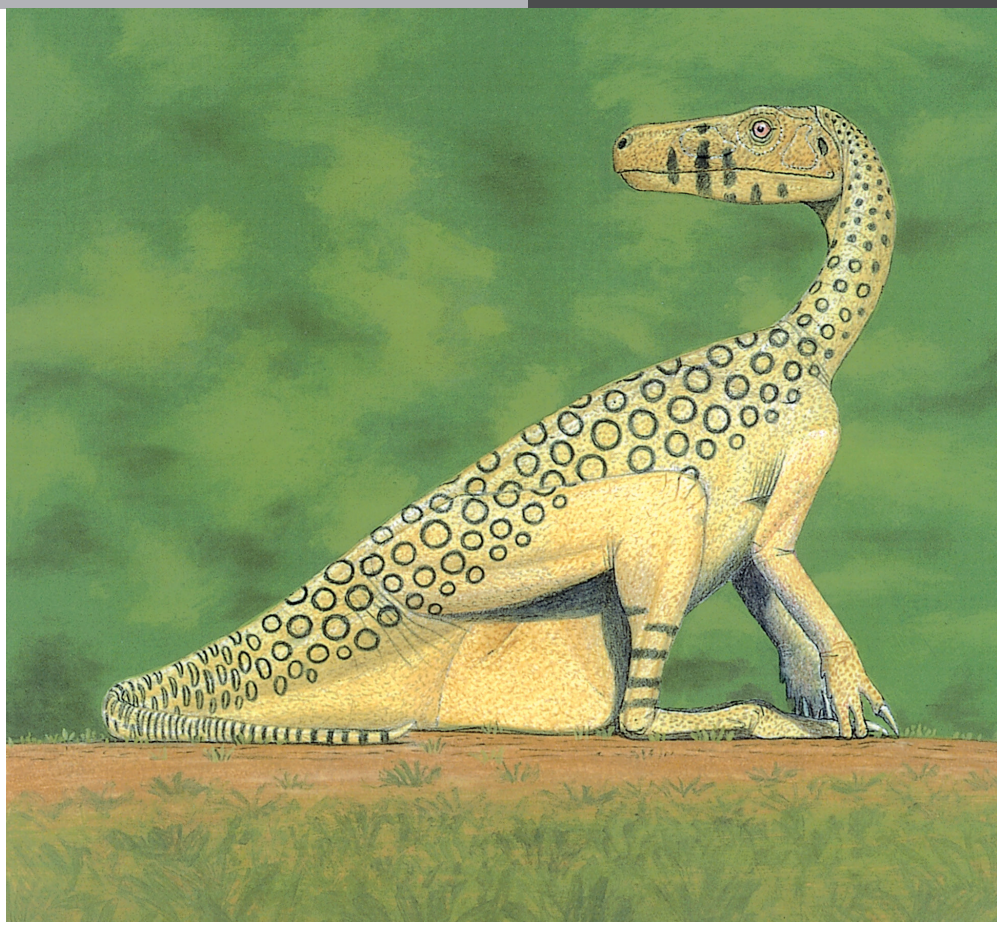
Herrerasaurus (Gnathovorax) cabreirai
— 3 m (9.5 ft) TL, 60 kg (130 lb)
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Pubis a little retroverted.
AGE Late Triassic, middle Carnian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; middle Santa Maria.
HABITS Large game hunter.
NOTES Reliable restoration of incompletely described skeleton not yet possible. May be an ancestor of *H.ischigualastensis*.



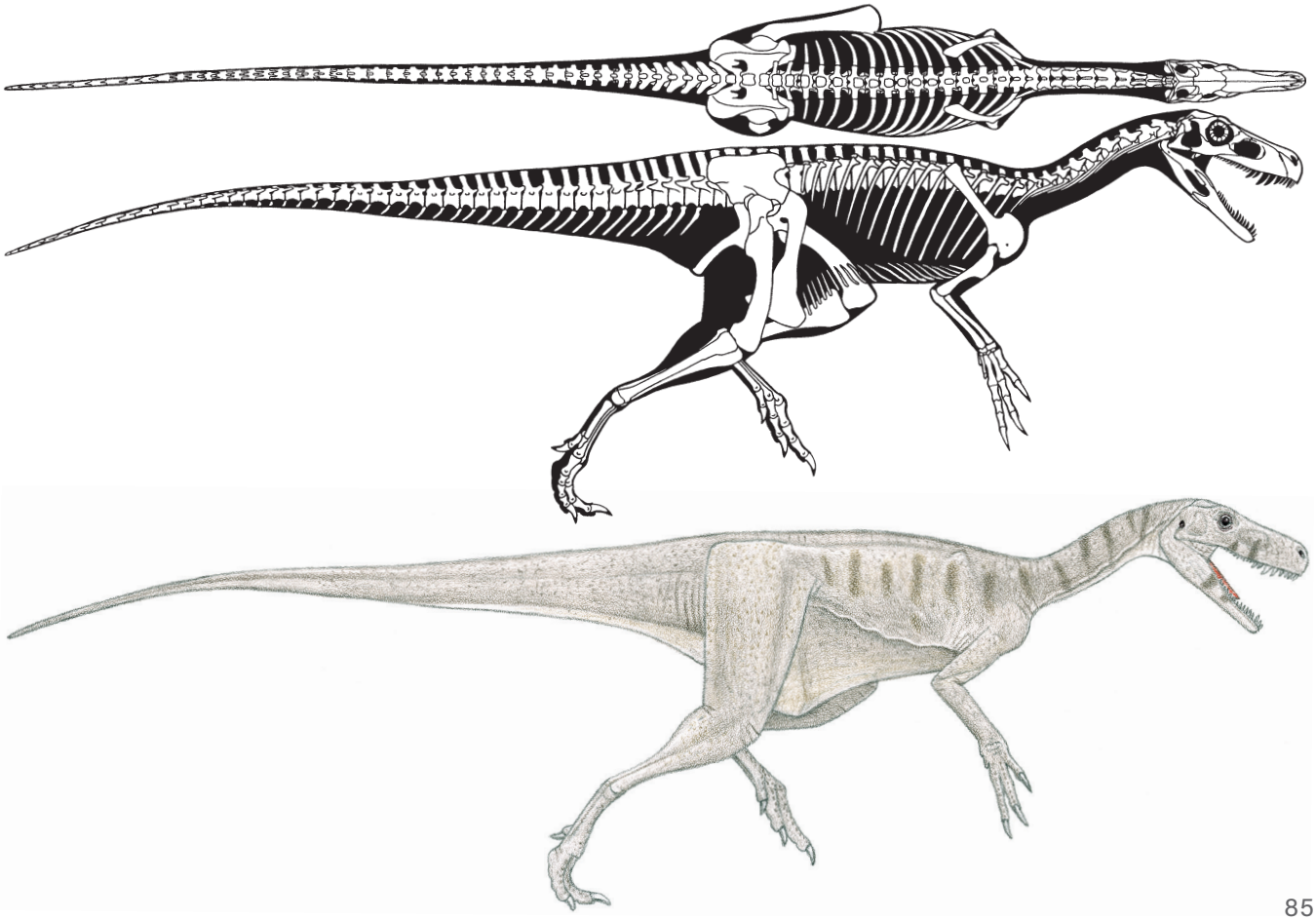
Staurikosaurus pricei

Herrerasaurus (*Gnathovorax*) *cabreirai*

Herrerasaurus ischigualastensis
— 4.5 m (15 ft) TL, 220 kg (450 lb)
FOSSIL REMAINS Two complete skulls and several partial skeletons.
ANATOMICAL CHARACTERISTICS **PUBIS A LITTLE RETROVERTED.**
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Northern Argentina; lower Ischigualasto.
HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.
HABITS Large game hunter.
NOTES The classic archaic predaceous dinosaur; includes *Frenguellisaurus ischigualastensis* and *Ischisaurus cattoi*. Has been considered a very basal saurischian, paxdinosaur, or theropod.



Herrerasaurus ischigualastensis



Eodromaeus murphi

Eodromaeus murphi
— 1.8 m (6 ft) TL, 5.5 kg (12 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Somewhat robust. Pubis a little procumbent.
AGE Late Triassic, late Carnian and/or earliest Norian.
DISTRIBUTION AND FORMATION/S Northern Argentina; lower Ischigualasto.
HABITAT Seasonally well-watered forests, including dense stands of giant conifers.
NOTES Has been considered a very basal saurischian, theropod, or ornithoscelid.

THEROPODS

SMALL TO GIGANTIC PREDATORY TO HERBIVOROUS DINOSAURS, FROM THE LATE TRIASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS All obligatory bipeds, otherwise very variable. Head size and shape variable, skull bones usually somewhat loosely attached to one another, usually extra joint at middle of lower jaw, eyes normally large, usually if not always supported by internal bone ring, teeth from large serrated blades to absent. Necks long to fairly short, usually S-curved to greater or lesser extent, moderately flexible. Trunk vertebral series short and stiff. Tails from long and very flexible to very short. Arms very long to severely reduced, fingers four to one, fingers long and slender to short, sharp claws from large to absent. Pelves moderate in size to very large, legs flexed at all sizes, long, main toes four to three; footprints confirm that trackway gauge was very narrow. Brains vary from reptilian in size and form to those of birds.
ENERGETICS Thermophysiology moderate to very high energy.
HABITATS Very diverse, from sea level to highlands, from tropics to polar winters, from arid to wet.
HABITS Diets ranged from classic hunting with opportunistic scavenging to full herbivory. Small adults and juveniles with long arms and hook-clawed fingers able to climb. Enormous numbers of trackways laid down along watercourses show that many theropods of all sizes spent considerable time patrolling shorelines and using them to travel. Adept surface swimmers, so able to cross large bodies of water, may have had some diving ability.
NOTES Already somewhat birdlike at the beginning, generally became increasingly so with time, especially among some advanced groups that include the direct ancestors of birds.

BASOTHEROPODS

SMALL TO MODERATELY LARGE THEROPODS, LIMITED TO THE LATE TRIASSIC.

ANATOMICAL CHARACTERISTICS Lightly built. Heads moderately large, fairly narrow, teeth serrated blades. Necks moderately long, only gently S-curved. Tails long. Arms and four-fingered hands moderately long, claws well developed. Pelves short but deep, four load-bearing toes. Beginnings of birdlike respiratory system possibly present. Brains reptilian.
HABITS Pursuit predators. Head and arms primary weapons. Jaws and teeth delivered slashing wounds to disable muscles and cause bleeding, shock, and infection. Arms used to hold on to and control prey, possibly delivered slashing wounds.
ENERGETICS Thermophysiology probably moderate, energy levels and food consumption probably lower than in most more derived dinosaurs.

NOTES Basotheropods are basal theropods excluding avepods. May have included some of the above basal dinosaurs. The most basal theropods, these briefly existing early theropods were apparently not able to compete with the more sophisticated avepods. Absence from at least some other continents probably reflects lack of sufficient sampling.

Daemonosaurus chauliodus

— Adult size uncertain

FOSSIL REMAINS Nearly complete skull and minority of skeleton.

ANATOMICAL CHARACTERISTICS Head deep, subtriangular, snout short, eyes large, upper teeth very large, those in front procumbent.

AGE Late Triassic, Rhaetian.

DISTRIBUTION AND FORMATION/S New Mexico; probably upper Chinle.

HABITS Probably caught fish as well as land prey.

NOTES Ontogenetic stage of fossil uncertain, so how much unusual form is juvenile or distinctive is also uncertain.

Tawa hallae

— 2.5 m (6 ft) TL, 16 kg (35 lb)

FOSSIL REMAINS Nearly complete skull and majority of a few skeletons, almost completely known.

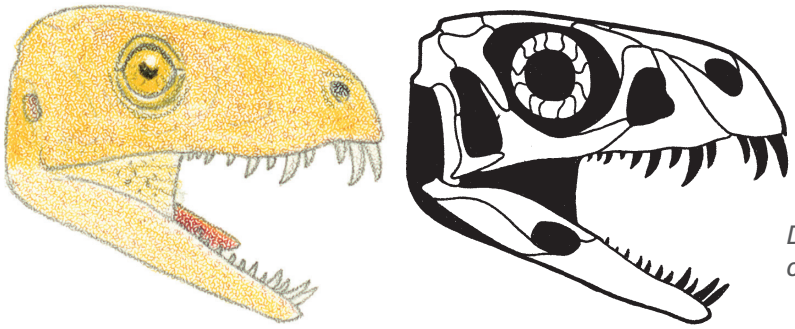
ANATOMICAL CHARACTERISTICS Snout pointed, upper teeth large. Unfused narrow sternal plates present. Pubis vertical, leg slender.

AGE Late Triassic, middle Norian.

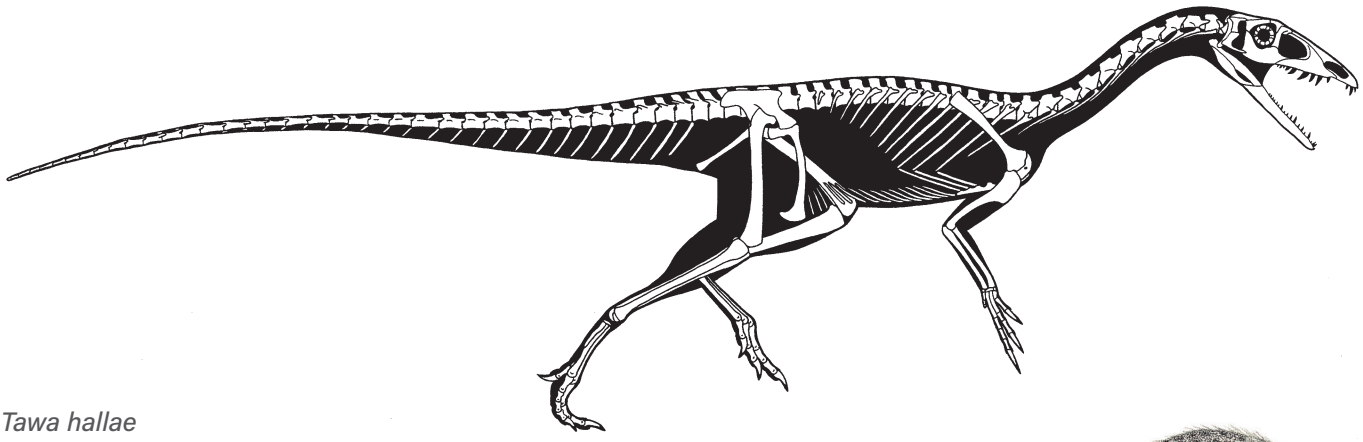
DISTRIBUTION AND FORMATION/S New Mexico; upper Chinle.

HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.

HABITS Probably fastest of known basal dinosaurs.



Daemonosaurus chauliodus



Tawa hallae

AVEPODS

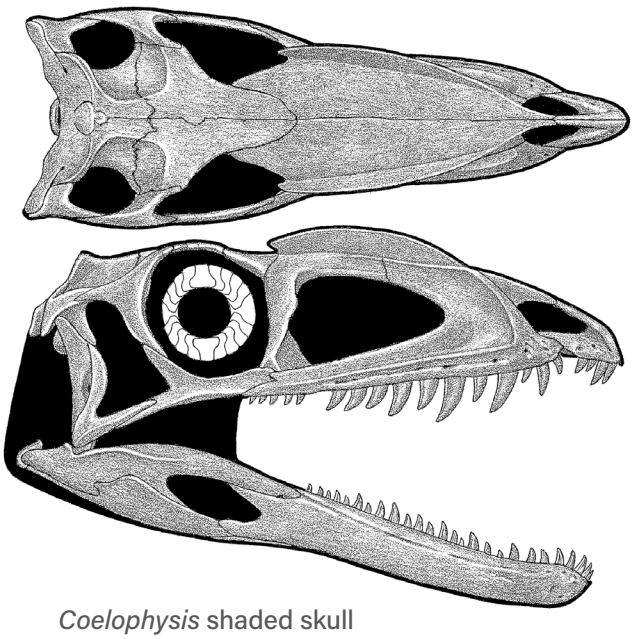
SMALL TO GIGANTIC THREE-TOED PREDATORY AND HERBIVOROUS THEROPODS, MOST PREDATORS, FROM THE LATE TRIASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Head size and shape variable, teeth large and bladed to absent. Necks long to fairly short. Trunks short, stiff. Tails long to very short. Fused furculas often present, arm very long to severely reduced, fingers four to one, usually three, fingers long and slender to short, claws large to reduced. Pelves large, legs long, usually three main toes, inner toe a short hallux, sometimes four load-bearing toes, or two. Skeletons pneumatic, birdlike, air sac–ventilated respiratory system developing. Brains vary from reptilian in size and form to those of birds.
ENERGETICS Energy levels and food consumption probably similar to those of ratites up until other birds.
HABITS Diets ranged from classic hunting in most to full herbivory in some specialized groups. Adept surface swimmers, so able to cross large bodies of water, hard pressed or unable to completely submerge because of pneumatic bodies.
NOTES Theropods lacking contact of metatarsal 1 with ankle, or ancestors with same that are in the clade that includes extant birds; contains both neotheropods and taxa more basal than that with the feature. Distinctly birdlike from the start, tridactyl foot most of all.

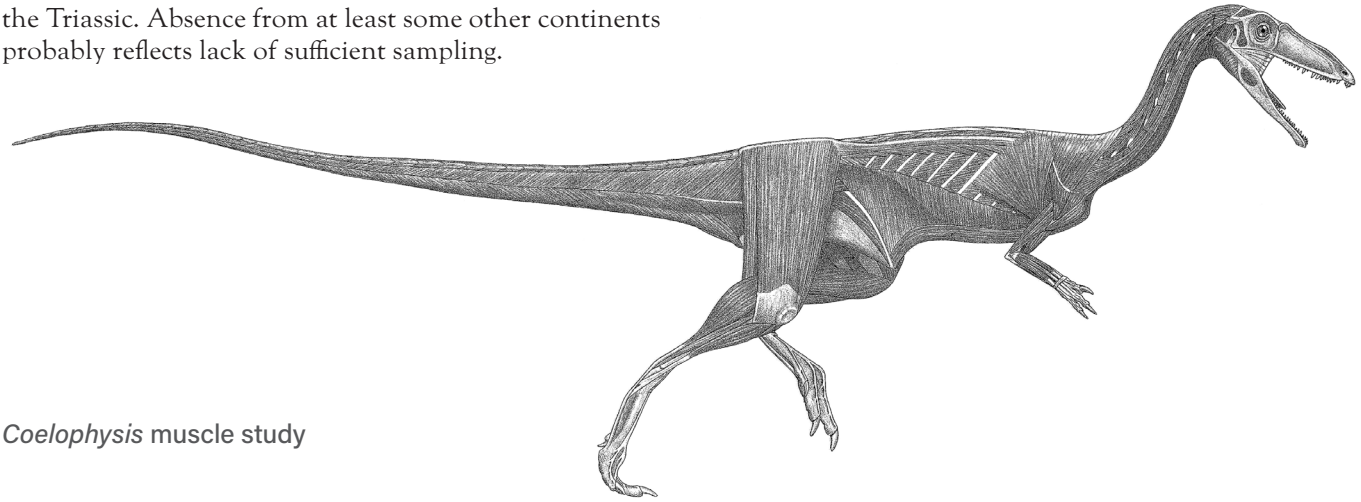
— PODOKESAUROIDS

SMALL TO LARGE AVEPODS, LIMITED TO THE LATE TRIASSIC AND EARLY JURASSIC, NORTHERN HEMISPHERE AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Generally lightly built. Heads long, snout pointed, narrow, indentation at front of upper jaw often present, lightly constructed paired crests over snout often present, teeth bladed and serrated. Necks long. Trunks not deep. Tails quite long, slender. Arms moderately long, fingers moderately long, claws modest in size. Pelves moderately large. Brains reptilian. Skeletal pneumaticity partly developed, so birdlike respiratory system developing.
ONTOGENY Growth rates moderate.
HABITS Although predominantly fast pursuit predators, snaggly teeth at tip of kinked upper jaw indicate these were also fishers. Crests when present too delicate for headbutting; for lateral visual display within the species, may or may not have been brightly colored at least during breeding season.
NOTES Podokesauroids are basal avepods excluding averostrans. Group splittable into a number of subdivisions including coelophysoids; many divisions are uncertain. The most basal avepods, first large examples show avepod theropods reached considerable size as early as the Triassic. Absence from at least some other continents probably reflects lack of sufficient sampling.



Coelophysis shaded skull



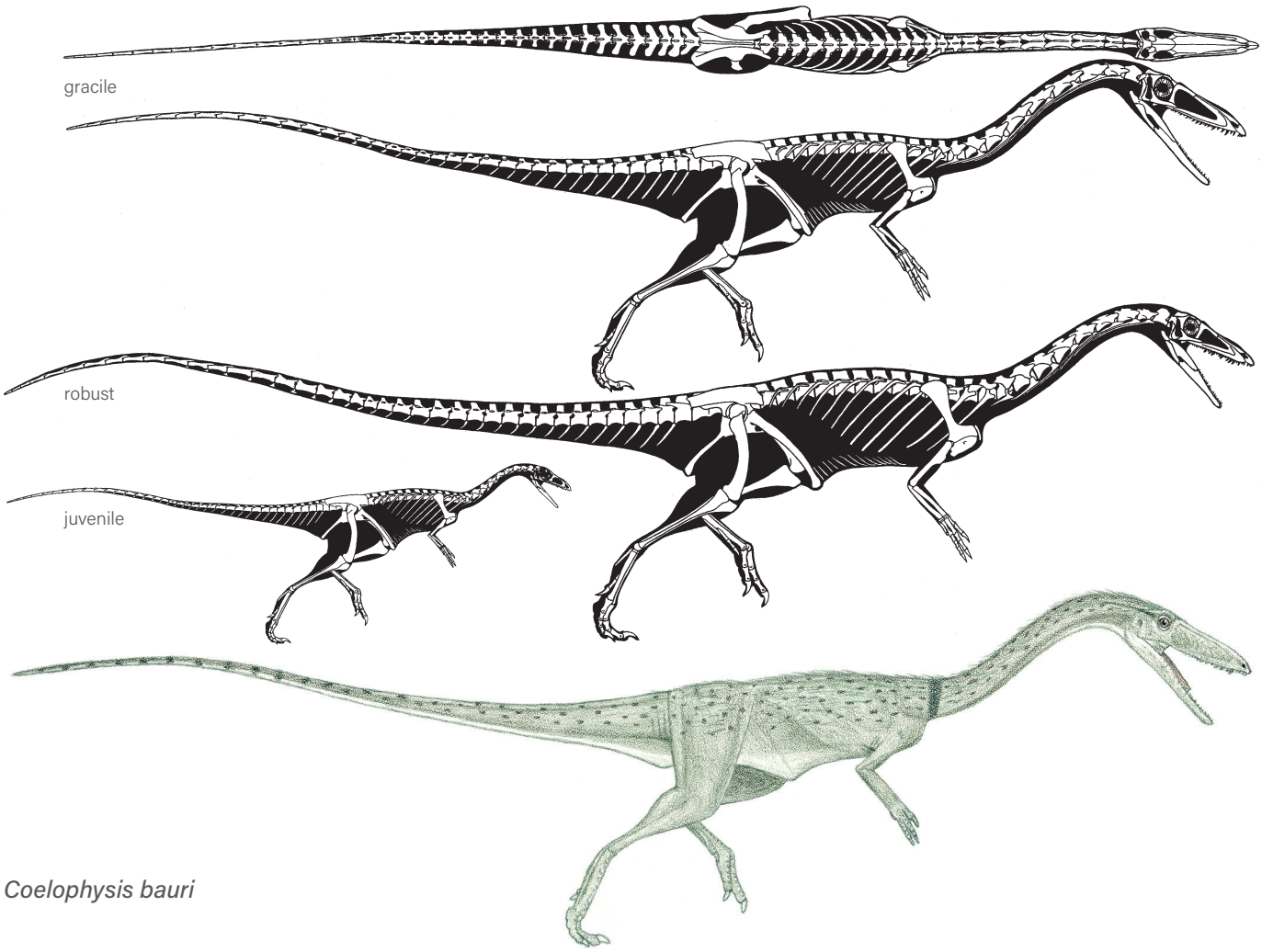
Coelophysis muscle study

Dracoraptor hanigani
— 1.8 m (6 ft) TL, 4 kg (10 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Apparently standard for small podokesauroids.
AGE Early Jurassic, earliest Hettangian.
DISTRIBUTION AND FORMATION/S Wales; middle Blue Lias.
NOTES Appears to be the most basal member of the group, probably coelophysoid. Found as drift in nearshore interisland marine sediments.

Procompsognathus triassicus
— 1.1 m (3.5 ft) TL, 1 kg (2 lb)
FOSSIL REMAINS Poorly preserved partial skeleton with possible skull.
ANATOMICAL CHARACTERISTICS Apparently standard for small podokesauroids.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Southern Germany; middle Lowenstein.
NOTES Remains that belong to this taxon not entirely certain. Smallest known member of the group. Name incorrectly implies an ancestral relationship with the very different *Compsognathus*. Probable coelophysid. Whether head crests were present is uncertain.

Lucianovenator bonoi
— 4 m (13 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Minority of four skeletons.
ANATOMICAL CHARACTERISTICS Apparently standard for small podokesauroids.
AGE Late Triassic, late Norian or Rhaetian.
DISTRIBUTION AND FORMATION/S Northwestern Argentina; upper Quebrada del Barro.
HABITAT/S Semiarid.
NOTES Probable coelophysid. Whether head crests were present is uncertain.

Coelophysis bauri
— 3 m (10 ft) TL, 25 kg (50 lb)
FOSSIL REMAINS Hundreds of skulls and skeletons, many complete, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Very lightly built and gracile, overall very long trunked. Head long and shallow, bite not powerful, crests absent, teeth numerous and small. Neck long and slender.
AGE Late Triassic, Rhaetian.



Coelophysis bauri

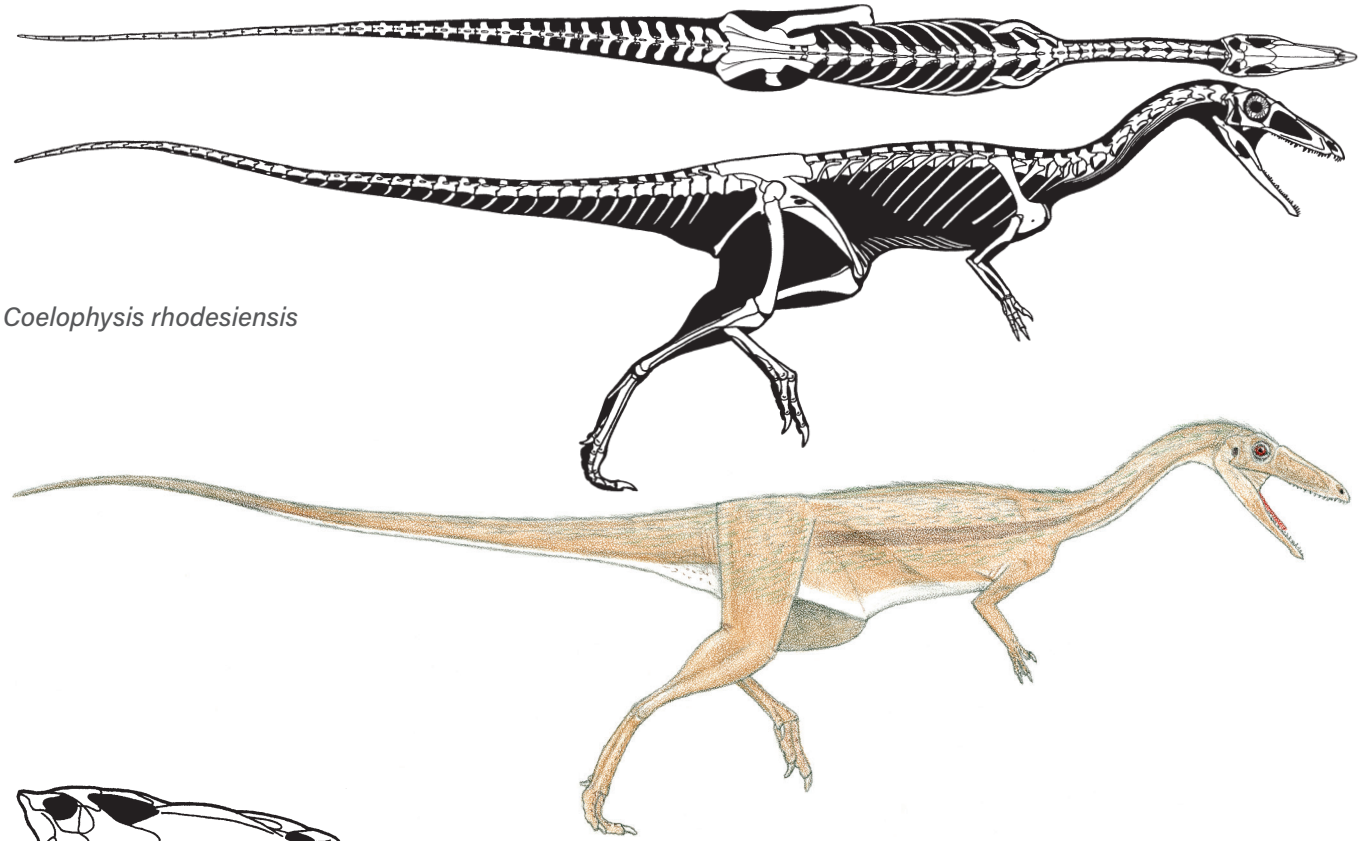
DISTRIBUTION AND FORMATION/S New Mexico; uppermost Chinle.
HABITS Predominantly small game hunter but may have occasionally attacked larger prosauropods and herbivorous thecodonts.
NOTES The classic early avepod theropod. In accord with a decision of the committee that handles taxonomic issues, the fossil that the taxon is based on was shifted from inadequate remains in the Chinle to a complete fossil from the famous Ghost Ranch Quarry. A very small element may be fifth metacarpal of hand, or a lateral distal carpal. How hundreds of skeletons came to be concentrated in the quarry remains unsettled.

Coelophysis rhodesiensis

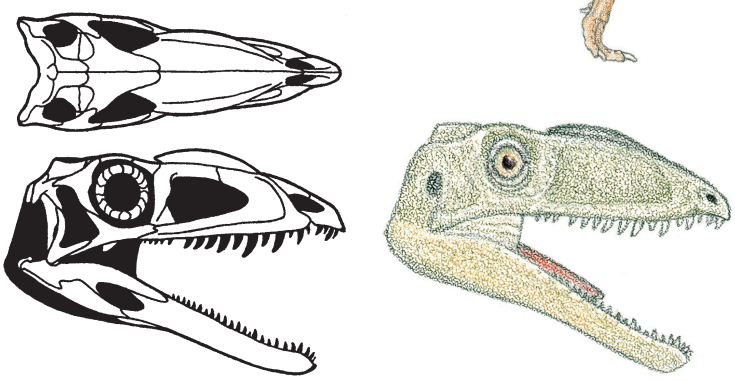
— 2.2 m (7 ft) TL, 14 kg (30 lb)
FOSSIL REMAINS Hundreds of skulls and skeletons, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Same as *C. bauri* except leg longer relative to body.
AGE Early Jurassic, Hettangian.
DISTRIBUTION AND FORMATION/S Zimbabwe; Forest Sandstone.
HABITAT/S Desert with dunes and oases.
HABITS Same as *C. bauri*, except thecodonts not present.
NOTES Originally *Syntarsus*, that name preoccupied by an insect; species is now often accepted as a species of the very similar *Coelophysis*; apparent absence of small fifth metacarpal may be due to smaller fossil sample. Whether remains from other South African formations belong to this species is uncertain.

Coelophysis kayentakatae

— 2.5 m (9 ft) TL, 30 kg (60 lb)
FOSSIL REMAINS Complete skull and minority of skeleton, other partial remains.
ANATOMICAL CHARACTERISTICS Head fairly deep, snout crests well developed, teeth fairly large and less numerous than in other *Coelophysis*.



Coelophysis rhodesiensis



Coelophysis kayentakatae

AGE Early Jurassic, early Sinemurian.
DISTRIBUTION AND FORMATION/S Arizona; middle Kayenta.
HABITAT/S Semiarid.
HABITS More robust head and larger teeth indicate this species tended to hunt larger game than other *Coelophysis*.
NOTES Originally in *Syntarsus*.

Podokesaurus (or *Coelophysis*) *holyokensis*

— 1 m (3 ft) TL, 1 kg (2 lb)
FOSSIL REMAINS Partial skeleton, possibly juvenile.
ANATOMICAL CHARACTERISTICS Standard for small coelophysoids.
AGE Early Jurassic, Pliensbachian or Toarcian.
DISTRIBUTION AND FORMATION/S Massachusetts; Portland?
HABITAT/S Semiarid rift valley with lakes.
NOTES Lost in a fire; the original location and age of this fossil are not entirely certain. Not known whether head crests were present.

Panguraptor lufengensis

— Adult size uncertain
FOSSIL REMAINS Majority of skull and skeleton, probably a subadult.
ANATOMICAL CHARACTERISTICS Standard for small coelophysoids, snout crests absent.
AGE Early Jurassic, earliest Hettangian.
DISTRIBUTION AND FORMATION/S Southwestern China; lower lower Lufeng.
NOTES Probable coelophysid.

Segisaurus halli

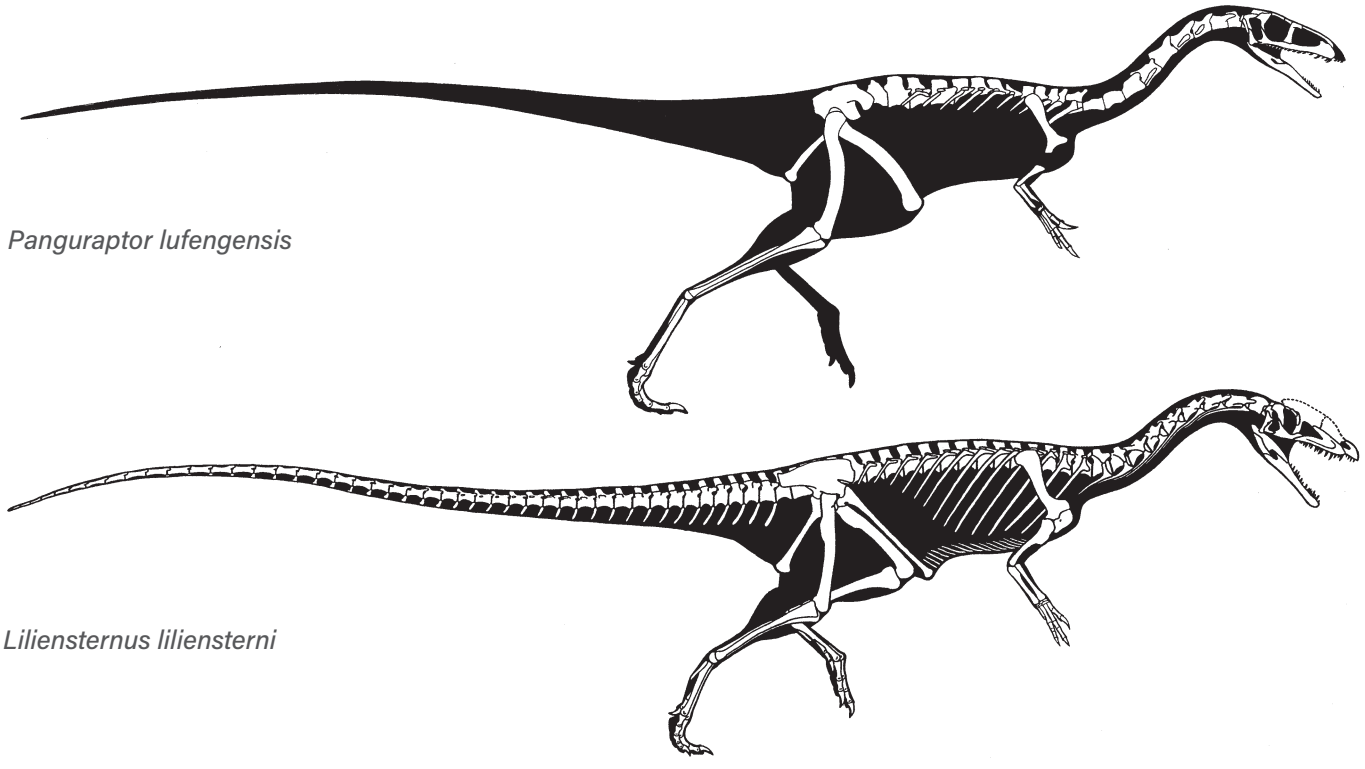
— Adult size uncertain
FOSSIL REMAINS Partial skeleton, large juvenile.
ANATOMICAL CHARACTERISTICS Standard for small coelophysoids.
AGE Early Jurassic, Pliensbachian or Toarcian.
DISTRIBUTION AND FORMATION/S Arizona; Navajo Sandstone.
HABITAT/S Dune desert with oases.
HABITS Largely a small game hunter, probably small prosauropods and ornithischians also.
NOTES Probable coelophysid. Not known whether head crests were present.

Gojirasaurus quayi

— 6 m (20 ft) TL, 150 kg (350 lb)
FOSSIL REMAINS Small portion of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S New Mexico; Cooper Canyon.
HABITAT/S Well-watered forests, including dense stands of giant conifers.
NOTES Remains that belong to this taxon uncertain. Probable coelophysoid. Not known whether head crests were present.

Liliensternus liliensterni

— 5.2 m (17 ft) TL, 140 kg (300 lb)
FOSSIL REMAINS Majority of skull and two skeletons.
ANATOMICAL CHARACTERISTICS Lightly built like smaller coelophysoids.



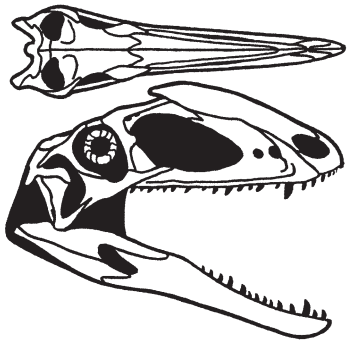
Panguraptor lufengensis

Liliensternus liliensterni

AGE Late Triassic, late Norian.
DISTRIBUTION AND FORMATION/S Central Germany; Knollenmergel.
NOTES Probable coelophysoid. Not known whether head crests were present.

Lophostropheus airelensis
— Adult size uncertain
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Latest Triassic and/or Early Jurassic, late Rhaetian and/or early Hettangian.
DISTRIBUTION AND FORMATION/S Northern France; Moon-Airel.

Zupaysaurus rougieri
— 6 m (20 ft) TL, 250 kg (550 lb)
FOSSIL REMAINS Almost complete skull and partial skeleton.

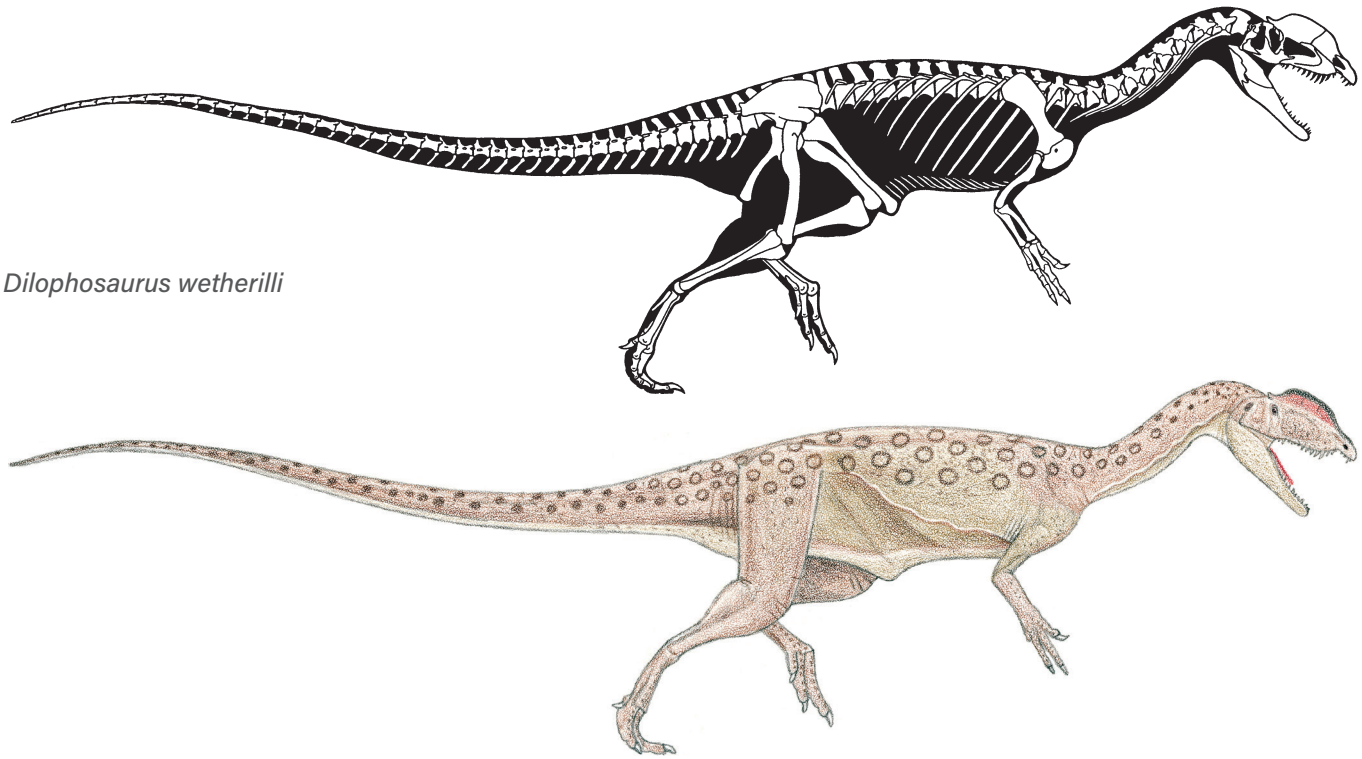


Zupaysaurus rougieri

ANATOMICAL CHARACTERISTICS Head moderately deep, snout very large, adorned with well-developed paired crests, teeth not large.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Los Colorados.
HABITAT/S Seasonally wet woodlands.
HABITS Big game hunter.
NOTES When first described this was considered to be the earliest tetanuran theropod, but other research indicates it is a podokesauroid related to *Dilophosaurus*.

Dracovenator regenti
— 6 m (20 ft) TL, 250 kg (550 lb)
FOSSIL REMAINS Two partial skulls, juvenile and adult.
ANATOMICAL CHARACTERISTICS Snout crests apparently not large, teeth large.
AGE Early Jurassic, late Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.
HABITS Big game hunter.

Dilophosaurus wetherilli
— 7 m (22 ft) TL, 285 kg (600 lb)
FOSSIL REMAINS Majority of several skulls and skeletons.
ANATOMICAL CHARACTERISTICS More robustly constructed than smaller coelophysoids. Head large, deep, snout crests large, teeth large.
AGE Early Jurassic, Hettangian or Sinemurian.



Dilophosaurus wetherilli

DISTRIBUTION AND FORMATION/S Arizona; lower Kayenta.
HABITAT/S Semiarid.
HABITS Big game hunter.

NOTES Exact shape of crest uncertain. This, *Liliensternus*, *Zupaysaurus*, and *Dracovenator* may form family Dilophosauridae, or these may form a group close to but outside podokesauroids.

Dilophosaurus wetherilli

— AVEROSTRANS

SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS AVEPODS FROM THE EARLY JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Nasal sinuses better developed. Brains reptilian to avian. Birdlike respiratory system better developed. Pelvic plate large.

— CERATOSAURS

MEDIUM-SIZED TO LARGE PREDATORY AVEROSTRANS FROM THE JURASSIC OF THE AMERICAS, EUROPE, AND AFRICA.

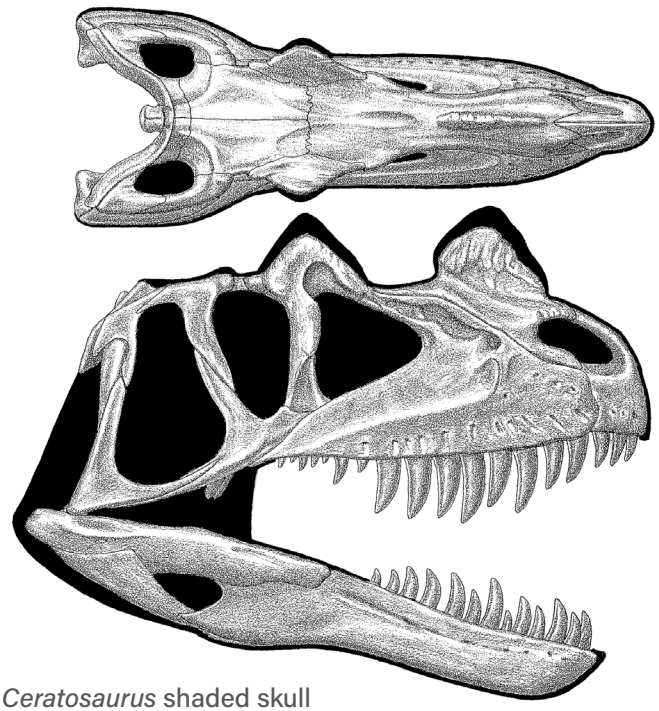
ANATOMICAL CHARACTERISTICS Uniform. Stoutly built. Four fingers. Tails long.
HABITS Ambush and pursuit big game hunters.
NOTES May include fragmentary *Bebesaurus liasicus*, *Saltriovenator zanellai*, and *Genyodectes serus*; the latter from Aptian of Argentina may indicate survival of group into Early Cretaceous. Absence from some continents may reflect lack of sufficient sampling.

Sarcosaurus woodi

— 3 m (10 ft) TL, 70 kg (150 lb)
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, latest Hettengian and/or earliest Sinemurian.
DISTRIBUTION AND FORMATION/S Wales; upper Blue Lias.
NOTES Includes *S. andrewsi*. Relationships with other avepods uncertain.

Ceratosaurus nasicornis

— 6 m (20 ft) TL, 570 kg (1,250 lb)
FOSSIL REMAINS Two skulls and some skeletons including a juvenile.
ANATOMICAL CHARACTERISTICS Head large, long, rectangular, narrow; large, narrow nasal horn, orbital hornlets large, subtriangular; teeth large. Tail deep and heavy. Arm and hand short. Leg not long. Single row of small, bony scales along back.
AGE Late Jurassic, latest Oxfordian and early Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado, Utah; lower and middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
ONTOGENY Growth rapid.
HABITS Ambush predators. Large bladed teeth indicate that this hunted large prey by delivering slashing wounds and that the head was a much more important weapon than the small arms. Deep tail used as powerful sculling organ while swimming. Nasal horn for display and possibly headbutting within the species. Armor row for display.

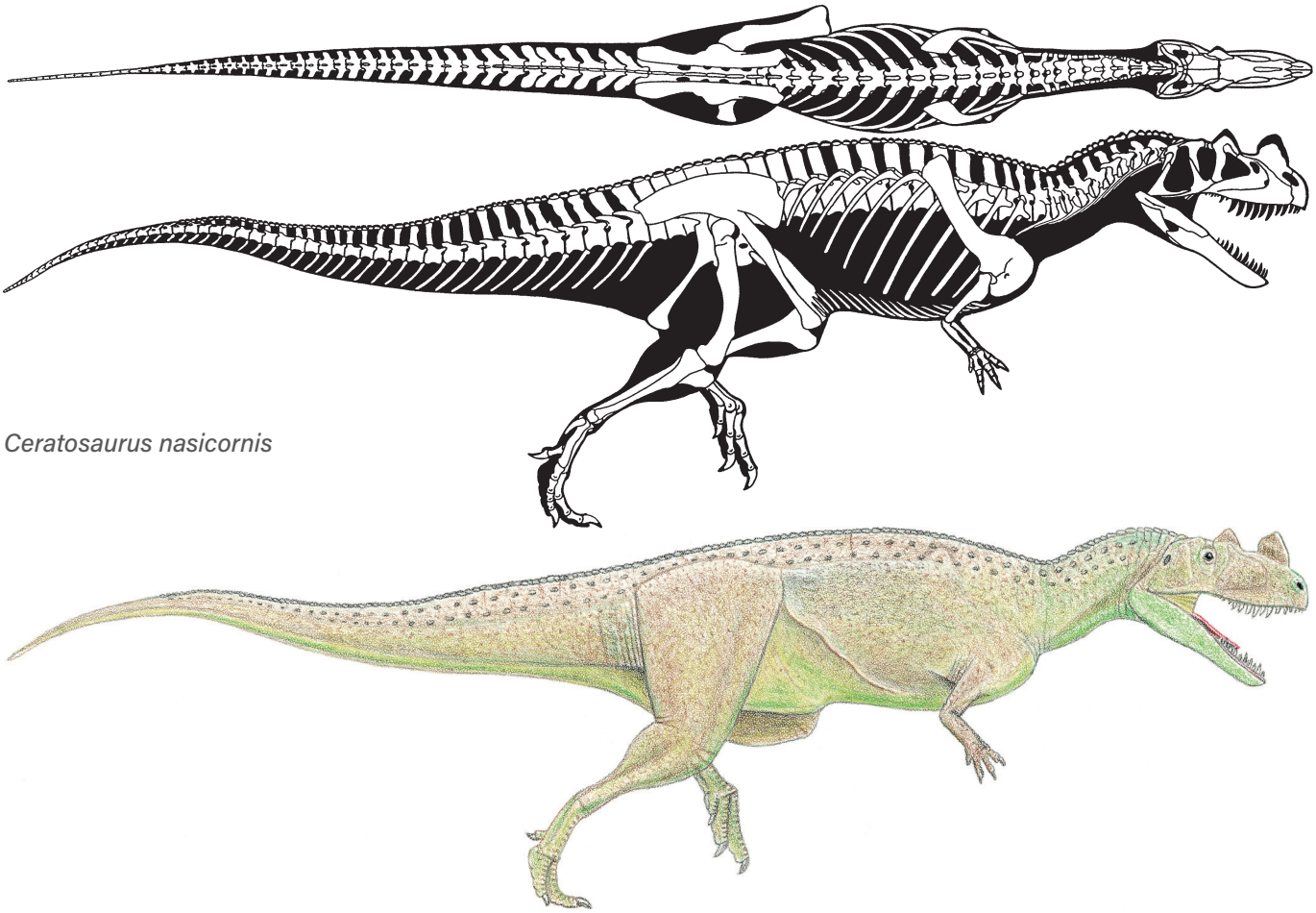


Ceratosaurus shaded skull

NOTES The species *C. magnicornis* is so similar that it appears to be a member of *C. nasicornis*, or it may represent a descendant of *C. nasicornis*. The only known theropods with any form of body armor.

Ceratosaurus dentisulcatus

— 7 m (21 ft) TL, 900 kg (2,000 lb)
FOSSIL REMAINS Part of a skull and skeleton.
ANATOMICAL CHARACTERISTICS Head deeper, lower jaw not as curved, and teeth not as proportionally large as in *C. nasicornis*.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Utah; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Similar to *C. nasicornis*.
NOTES It is uncertain whether *C. dentisulcatus* had a nasal horn or not. May have been the direct descendant of *C. nasicornis*.



Ceratosaurus nasicornis

Ceratosaurus nasicornis

Ceratosaurus? unnamed species

— 6 m (20 ft) TL, 600 kg (1,300 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late Kimmeridgian or early Tithonian.
DISTRIBUTION AND FORMATION/S Portugal; lower Lourinhã.
HABITAT/S Large, seasonally dry island with open woodlands.
NOTES Assignment by some researchers of this fossil to *C. dentisulcatus* is uncertain.

— ABELISAUROIDS

SMALL TO GIGANTIC AVEROSTRANS FROM THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, LARGELY LIMITED TO THE SOUTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Highly variable. Arms short, four fingers. Vertebrae often flat topped. Tails long. Pelves large. Birdlike respiratory system well developed.
NOTES Abelisaurs show that relatively archaic avepods were able to thrive in the Southern Hemisphere to the end of the dinosaur era as they evolved into specialized forms. Absence from Antarctica probably reflects lack of sufficient sampling.

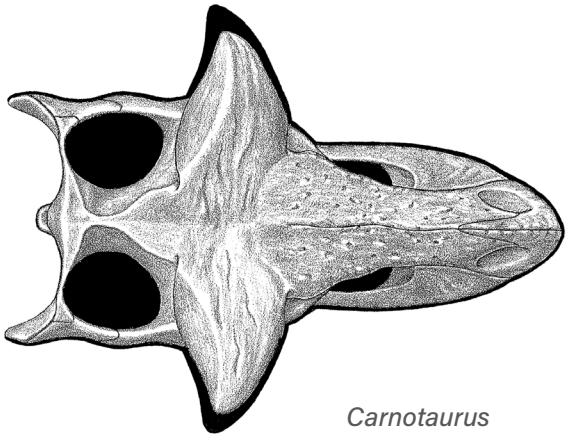
— ABELISAURIDS

MEDIUM-SIZED TO GIGANTIC ABELISAUROIDS OF THE MIDDLE JURASSIC TO THE END OF THE DINOSAUR ERA, LARGELY LIMITED TO THE SOUTHERN HEMISPHERE.

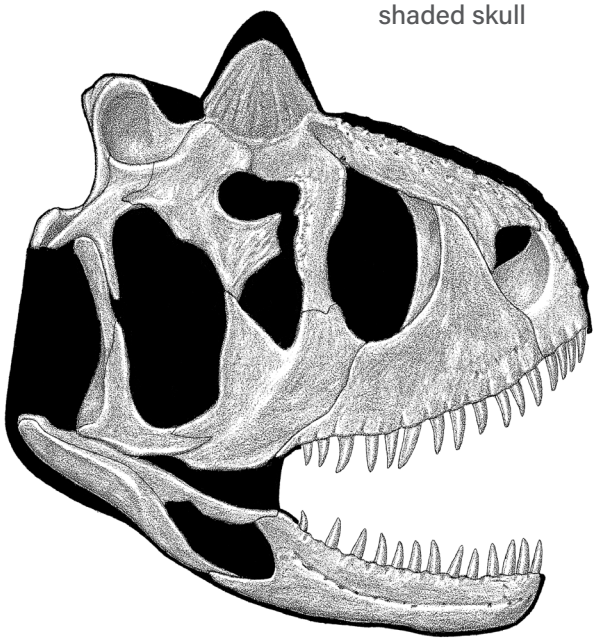
ANATOMICAL CHARACTERISTICS Fairly uniform. Heads heavily constructed, short and deep, lower jaws slender, teeth short and stout. Arms reduced. Tubercle scales set amid fairly large, flat scales.
HABITATS Seasonally dry to well-watered woodlands.
HABITS Ambush and pursuit big game hunters. Reduction of arms indicates that the stout head was the primary weapon, but how the combination of a deep, short skull, slender lower jaw indicating modest musculature, and short teeth functioned is obscure.
NOTES Fragmentary Late Cretaceous *Arcovenator escotae* from France may indicate presence of group in Northern Hemisphere.

Eoabelisaurus mefi

— 6.5 m (21 ft) TL, 850 kg (1,900 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Robustly built.
AGE Middle Jurassic, Aalenian and/or Bajocian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cañadón Asfalto.



Carnotaurus shaded skull



Spectrovenator ragei

Spectrovenator ragei

— Adult size uncertain
FOSSIL REMAINS Complete skull and partial skeleton, possibly juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; lower Quiricó.

Kryptops palaios
— Adult size uncertain
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Niger; Elrhaz, level uncertain.
HABITAT/S Coastal river delta.
NOTES The one fossil may be a large juvenile.

Rugops primus
— 6 m (20 ft) TL, 750 kg (1,600 lb)
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Snout very deep and robust, possible low paired crests on snout.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Niger; Echkar.

Xenotarsosaurus bonapartei
— 6 m (20 ft) TL, 750 kg (1,700 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Leg long and gracile.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.
HABITS Pursuit predator.

Majungasaurus crenatissimus
— 6 m (20 ft) TL, 730 kg (1,600 lb)
FOSSIL REMAINS Nearly perfect skull and extensive skeletal remains, almost completely known.
ANATOMICAL CHARACTERISTICS Low central horn above orbits. Leg stout, not elongated.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Madagascar; Maevarano.
HABITAT/S Seasonally dry floodplain with coastal swamps and marshes.
ONTOGENY Growth slow.
HABITS Some remains are under preparation. Used horn for display and probably headbutting within the species.

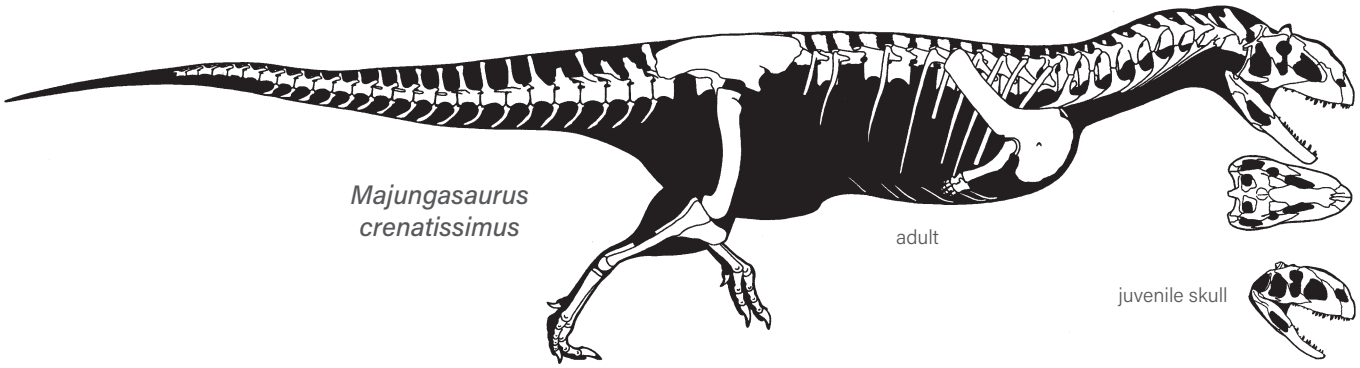
Ilokelesia aguadagrandensis
— 4 m (14 ft) TL, 200 kg (450 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Base of tail exceptionally broad.
AGE Late Cretaceous, late Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; middle Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Rajasaurus narmadensis
— 11 m (35 ft) TL, 5 tonnes
FOSSIL REMAINS Majority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Back of head adorned by central crest. Leg stout.
AGE Late Cretaceous, Maastrichtian.

Rugops primus

Rajasaurus narmadensis

Majungasaurus crenatissimus



DISTRIBUTION AND FORMATION/S Central India; Lameta.
HABITS Used horn for display and probably headbutting within the species.

Rahiolisaurus gujaratensis
— 8 m (27 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Less robust than *Rajasaurus*.
AGE Late Cretaceous, Maastrichtian.
DISTRIBUTION AND FORMATION/S Central India; Lameta.

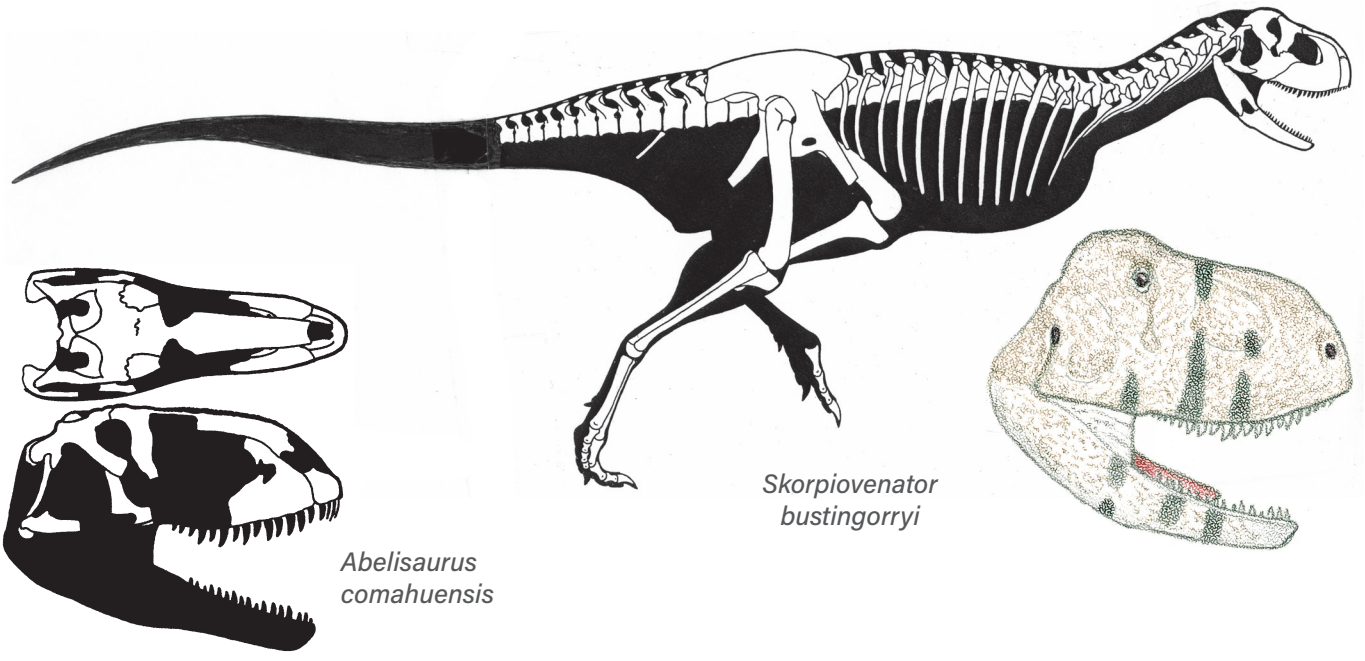
Ekrixinatosaurus novasi
— 6.5 m (21 ft) TL, 800 kg (1,800 lb)
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

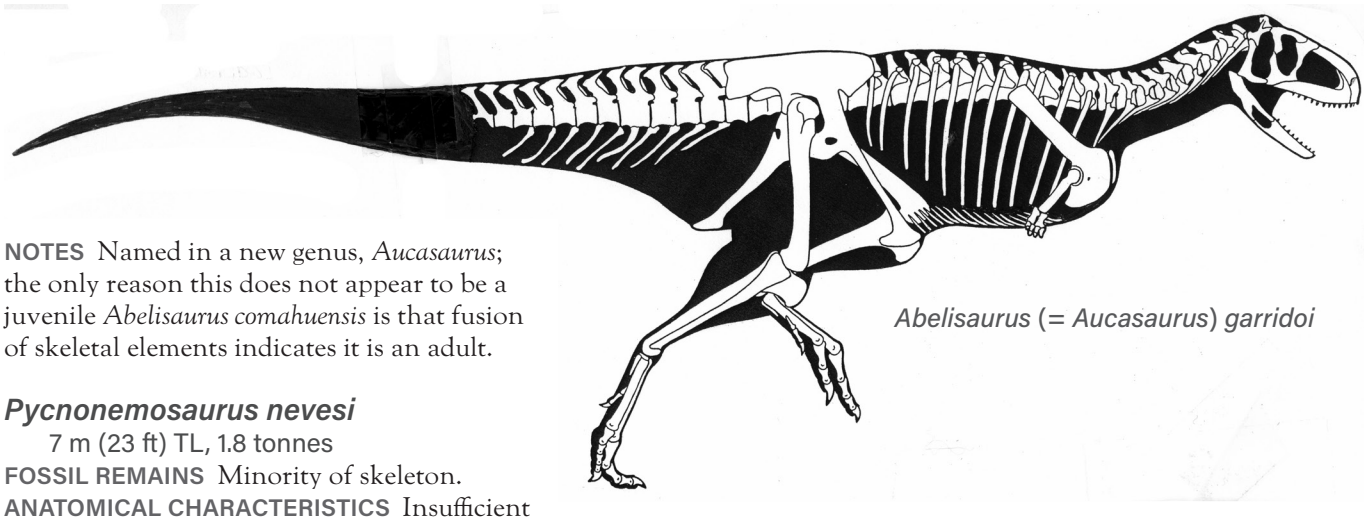
Skorpiovenator bustingorryi
— 7.5 m (25 ft) TL, 1.8 tonnes
FOSSIL REMAINS Complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Rugose area around eye socket. Leg long.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Huincul.
HABITAT/S Well-watered woodlands with short dry season.

Viavenator exxoni
— 5.5 m (18 ft) TL, 700 kg (1,500 lb)
FOSSIL REMAINS Majority of skull and partial skeleton, partial skeleton, at least one immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Central Argentina; upper Bajo de la Carpa.
NOTES *Llukalkan aliocranianus* may be juvenile of this species, skull proportions uncertain.

Abelisaurus comahuensis
— 10 m (30 ft) TL, 4 tonnes
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Head unadorned.
AGE Late Cretaceous, late Santonian and/or early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; Anacleto.
HABITAT/S Seasonally semiarid.

Abelisaurus (= *Aucasaurus*) *garridoi*
— 5.5 m (18 ft) TL, 740 kg (1,600 lb)
FOSSIL REMAINS Complete skull and nearly complete skeleton.
ANATOMICAL CHARACTERISTICS Head unadorned. Lower arm and hand atrophied. Leg long and gracile, inner toe reduced, toe claws small.
AGE Late Cretaceous, late Santonian and/or early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; upper Anacleto.
HABITAT/S Seasonally semiarid.
HABITS Pursuit predator able to chase prey at high speed.





Abelisaurus (= *Aucasaurus*) *garridoi*

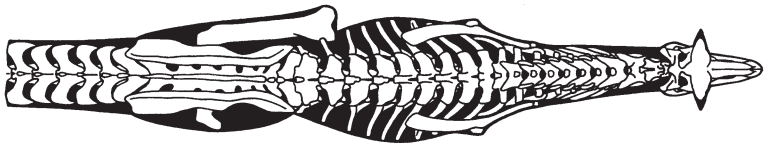
NOTES Named in a new genus, *Aucasaurus*; the only reason this does not appear to be a juvenile *Abelisaurus comahuensis* is that fusion of skeletal elements indicates it is an adult.

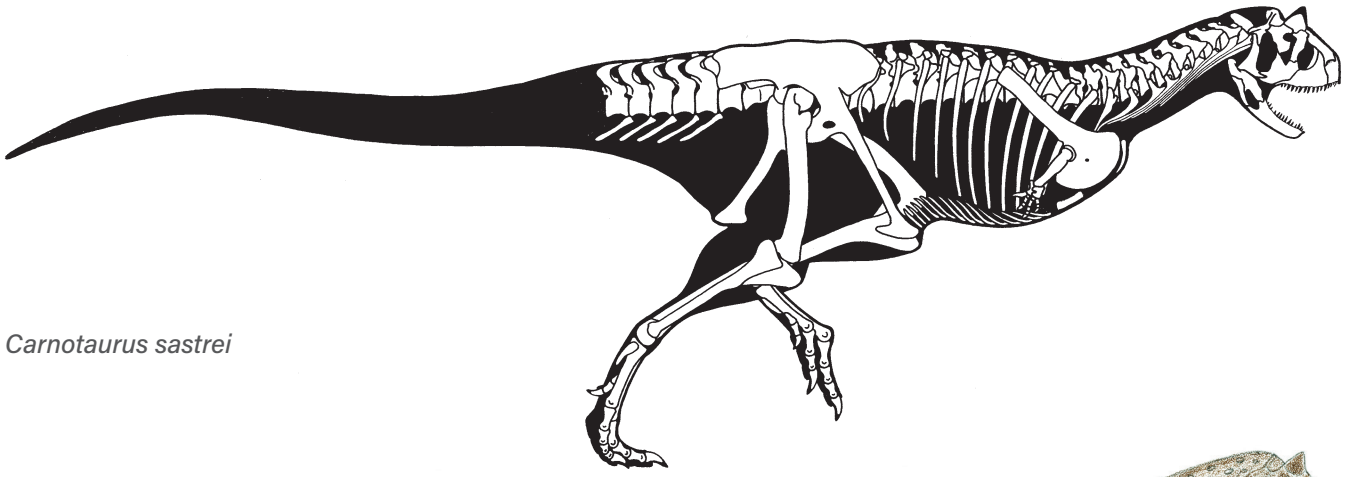
Pycnonemosaurus nevesi

7 m (23 ft) TL, 1.8 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southwestern Brazil; Bauro Group.

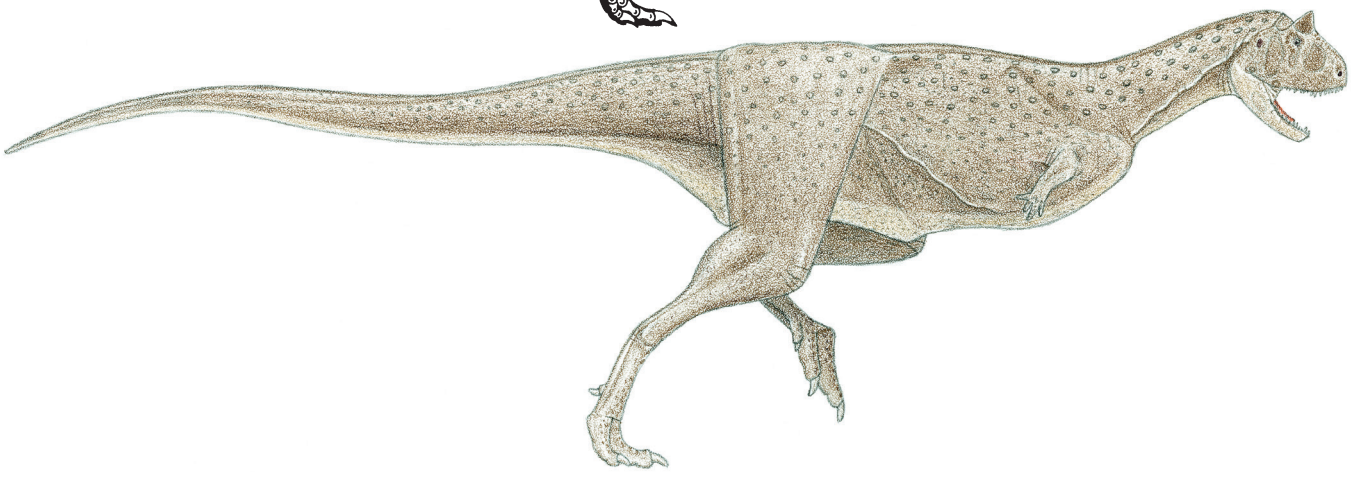
Carnotaurus sastrei

— 7.5 m (25 ft) TL, 2.2 tonnes
FOSSIL REMAINS Complete skull and majority of skeleton, skin patches.
ANATOMICAL CHARACTERISTICS Head very deep; large, stout brow horns directed sideways. Lower arm and hand atrophied.
AGE Late Cretaceous, Campanian or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; La Colonia.
HABITS Used horns for display, probably headbutting, and pushing within the species.
NOTES The most specialized known abelisaurid.





Carnotaurus sastrei



— NOASAURIDS

SMALL TO MEDIUM-SIZED ABELISAUROIDS OF THE LATE JURASSIC AND CRETACEOUS OF EURASIA, AFRICA, AMERICAS.

ANATOMICAL CHARACTERISTICS Highly variable. Most lightly constructed of the abelisaurs. Heads modest in size, not heavily built.

— ELAPHROSAURINES

MEDIUM-SIZED NOASAURIDS LIMITED TO THE LATE JURASSIC OF ASIA, AFRICA, AND NORTH AMERICA.

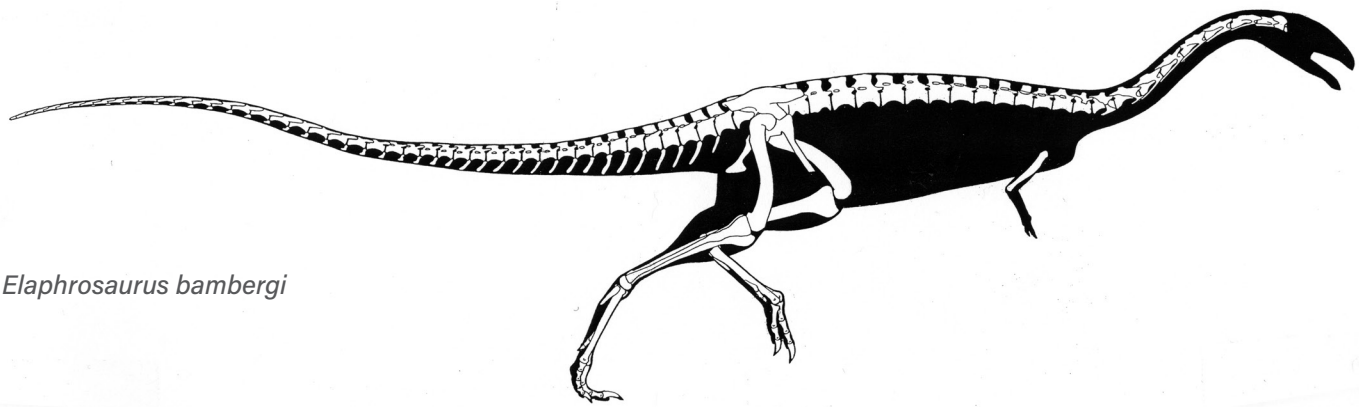
ANATOMICAL CHARACTERISTICS Overall build gracile. Heads modest in size, lightly built, at least adults toothless, with blunt beak. Arms short, slender, hands reduced, just two fingers in at least some examples. Pelves usually not highly enlarged, legs gracile.
HABITS Possibly omnivorous, predominantly herbivorous combined with some small animals and insects. Main defense speed, also kicks from legs.
NOTES These Jurassic ostrich mimics evolved feeding and running adaptations broadly similar to those of the even faster and longer-armed Cretaceous ornithomimids. Absence from at least some other continents probably reflects lack of sufficient sampling.

Spinostropheus gautieri
— 4 m (14 ft) TL, 80 kg (170 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Middle or early Late Jurassic.
DISTRIBUTION AND FORMATION/S Niger; Tiourarén.
HABITAT/S Well-watered woodlands.
NOTES Originally thought to be from the Early Cretaceous; researchers now place the Tiourarén in the later Jurassic.

Elaphrosaurus bambergi
— 6 m (20 ft) TL, 260 kg (450 lb)
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Trunk elongated and shallow. Tail quite long. Thigh narrow.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Tanzania; middle Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Remains from much later upper Tendaguru are not same taxon.

Elaphrosaurus? unnamed species
— 4.5 m (15 ft) TL, 100 kg (220 lb)
FOSSIL REMAINS Small portion of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, early and/or middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
NOTES It is uncertain whether these remains are the same genus as *Elaphrosaurus*, probably constitute two species over time.

Limusaurus inextricabilis
— 2 m (6 ft) TL, 17 kg (35 lb)
FOSSIL REMAINS About a dozen and a half skulls and skeletons, juvenile to adult, gastroliths present.



Elaphrosaurus bambergi

Limusaurus inextricabilis

ANATOMICAL CHARACTERISTICS Head moderately deep. Ossified sternum present. Two functional fingers. Inner toe reduced.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.
HABITS Presence of well-developed teeth in juveniles indicates shift from carnivory or omnivory to herbivory with growth.
NOTES Juveniles had teeth, juvenile skeleton not yet documented well enough to restore. Parallels tyrannosaurids in having just two fingers.

Berthasaura leopoldinae

— Adult size not certain
FOSSIL REMAINS Majority of skull and partial skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Goio-Erê.
NOTES Juvenile condition and incomplete remains hinder analysis. Lack of teeth suggest may be an elaphosaurine, large pelvis suggests a noasaurine. Juveniles toothless.

— NOASAURINES

MEDIUM-SIZED NOASAURIDS LIMITED TO THE CRETACEOUS OF AFRICA, SOUTH AMERICA, AND EUROPE.

ANATOMICAL CHARACTERISTICS Teeth present. Arms and hands not strongly reduced.
HABITS Predaceous, fishers.
NOTES Absence from at least some other continents probably reflects lack of sufficient sampling.

Bahariasaurus ingens and/or *Deltadromeus agilis*

— 11 m (35 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Shoulder girdle massively constructed. Leg long and gracile.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Morocco; Bahariya.
HABITAT/S Coastal mangroves.
HABITS Fast-running pursuit predator.
NOTES The relationships of *Bahariasaurus* and *Deltadromeus* to other theropods and each other are uncertain; the latter may be a juvenile of the former.

Ligabueino andesi

— 0.6 m (2 ft) TL, 0.4 kg (1 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Cretaceous, Barremian and/or early Aptian.
DISTRIBUTION AND FORMATION/S Western Argentina; La Amarga.
HABITAT/S Well-watered coastal woodlands with short dry season.
HABITS Small game hunter.
NOTES If not a juvenile, is one of the smallest theropods outside the birdlike airfoilans.

Velocisaurus unicus

— 1.5 m (5 ft) TL, 6 kg (15 lb)
FOSSIL REMAINS Two legs.
ANATOMICAL CHARACTERISTICS Leg long, slender, central shaft of upper foot strong with side bones slender.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Central Argentina; Bajo de la Carpa.
HABITS Good runner.

Masiakasaurus knopfleri
— 2 m (7 ft) TL, 12 kg (25 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Front teeth of lower jaw form a procumbent whorl and are long and weakly serrated; back teeth more conventional.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Madagascar; Maevarano.
HABITAT/S Seasonally dry floodplain with coastal swamps and marshes.
HABITS Hunted small prey, especially fish.

Noasaurus leali
— 1.5 m (5 ft) TL, 6 kg (15 lb)
FOSSIL REMAINS Minority of a skull and skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, probably early Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Lecho.
HABITS Pursuit predator.
NOTES It was thought that a large claw was a sickle-toe weapon like those of dromaeosaurids, but more likely it belonged to the hand.

Genusaurus sisteronis
— 3 m (10 ft) TL, 35 kg (70 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Southeastern France; Bevons Beds.
HABITAT/S Forested coastline.
NOTES Found as drift in nearshore marine sediments. Placement in noasaurids uncertain, if correct indicates that abelisauroids migrated to the Northern Hemisphere.

Vespersaurus paranaensis
— 2 m (7 ft) TL, 20 kg (50 lb)
FOSSIL REMAINS Partial remains.
ANATOMICAL CHARACTERISTICS Outer toes somewhat reduced relative to central toe.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Southern Brazil; Rio Paraná.
HABITAT/S Dune desert.
NOTES May have been semimonodactyl with central toe bearing almost all of animal's mass.

Masiakasaurus knopfleri

— TETANURANS

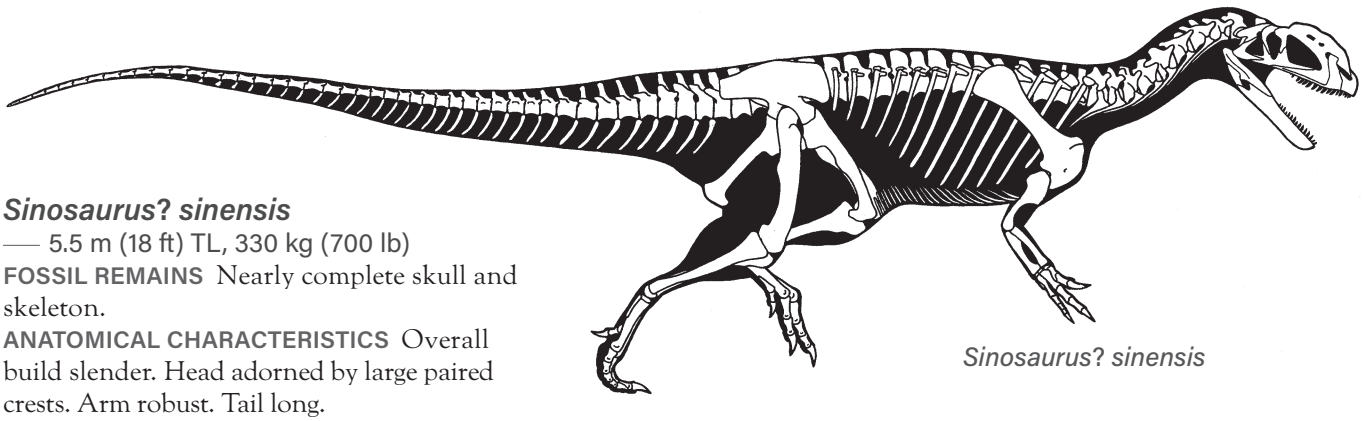
SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS AVEROSTRANS FROM THE MIDDLE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Arms very long to very reduced. Birdlike respiratory system usually better developed. Brains reptilian to avian.
ONTOGENY Growth moderately to very rapid.

— BASO-TETANURANS

SMALL TO LARGE PREDATORY AND HERBIVOROUS TETANURANS FROM THE JURASSIC.

HABITS Crests when present too delicate for headbutting; for visual display, may or may not have been brightly colored at least during breeding season.
NOTES The relationships of the following basal and usually partially known tetanurans are uncertain.



Sinosaurus? sinensis

Sinosaurus? sinensis

— 5.5 m (18 ft) TL, 330 kg (700 lb)
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Overall build slender. Head adorned by large paired crests. Arm robust. Tail long.
AGE Early Jurassic, early Hettangian.
DISTRIBUTION AND FORMATION/S Southwestern China; lower Lufeng.
HABITS Long crests for lateral display.
NOTES Broadly comparable in time, size, and overall appearance to similarly crested *Dilophosaurus*, it was assumed to be a member of the same genus, but detailed anatomy indicates this is a more derived tetanuran avepod. Because *S. triassicus?* is problematic, may not be that genus. May be direct ancestor of *S. triassicus?*, which is same genus.

Sinosaurus triassicus?

— 5.5 m (18 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS A complete and partial skulls.
ANATOMICAL CHARACTERISTICS Head adorned by large paired crests.
AGE Early Jurassic, middle Hettangian.
DISTRIBUTION AND FORMATION/S Southwestern China; upper Lufeng.
HABITS Long crests for lateral display.
NOTES Original fossils very fragmentary and may not be same species as complete skull.

Shuangbaisaurus anlongbaoensis

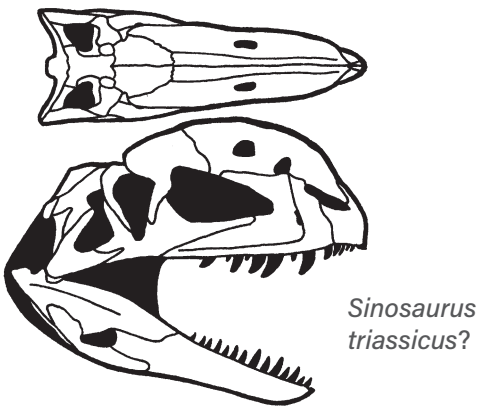
— 6 m (20 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Majority of distorted skull.
ANATOMICAL CHARACTERISTICS Head apparently adorned by paired crests.
AGE Early Jurassic, Pliensbachian.
DISTRIBUTION AND FORMATION/S Southwestern China; Fengjiahe.
NOTES Suggested placement in earlier *Sinosaurus* highly problematic.

Monolophosaurus jiangi

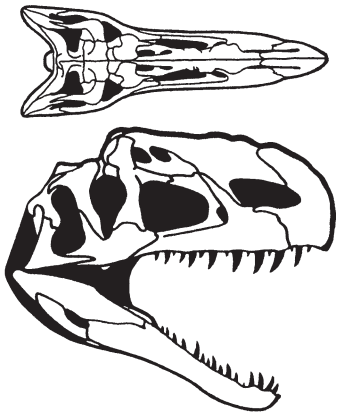
— 5.5 m (18 ft) TL, 540 kg (1,600 lb)
FOSSIL REMAINS Complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Overall build robust. Snout ridges united and enlarged into an enormous midline crest.
AGE Middle Jurassic, late Callovian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Shishugou.
HABITS Crest too delicate for headbutting, for visual display within the species.

Cryolophosaurus ellioti (see p.104)

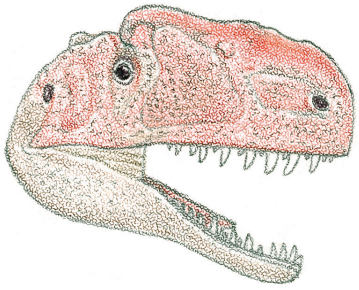
— 7 m (23 ft) TL, 775 kg (1,700 lb)
FOSSIL REMAINS Partial skull and two partial skeletons.
ANATOMICAL CHARACTERISTICS Overall build slender. Paired crests very low atop snout, above orbits arc toward middle and join to form large transverse crest. Arm robust.
AGE Early Jurassic, Sinemurian or Pliensbachian.
DISTRIBUTION AND FORMATION/S Central Antarctica; lower Hanson.



Sinosaurus triassicus?



Monolophosaurus jiangi



Cryolophosaurus ellioti

Chilesaurus diegosuarezi

HABITAT/S Polar forests with cold, dark winters.
HABITS Broad, tall crest for frontal display.
NOTES Largest known Early Jurassic avepod. The only theropod yet named from Antarctica, this reflects lack of more extensive exposed deposits and difficult research conditions.

Shidaisaurus jinae

— 6 m (20 ft) TL, 700 kg (1,600 lb)
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Neural spines form shallow sail over trunk and base of tail.
AGE Early Middle Jurassic.
DISTRIBUTION AND FORMATION/S Southwestern China; Chuanjie.

Xuanhanosaurus qilixiaensis

— 4.5 m (15 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Stoutly built. Arm and hand well developed.
AGE Late Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
HABITS Arms probably important in handling prey.

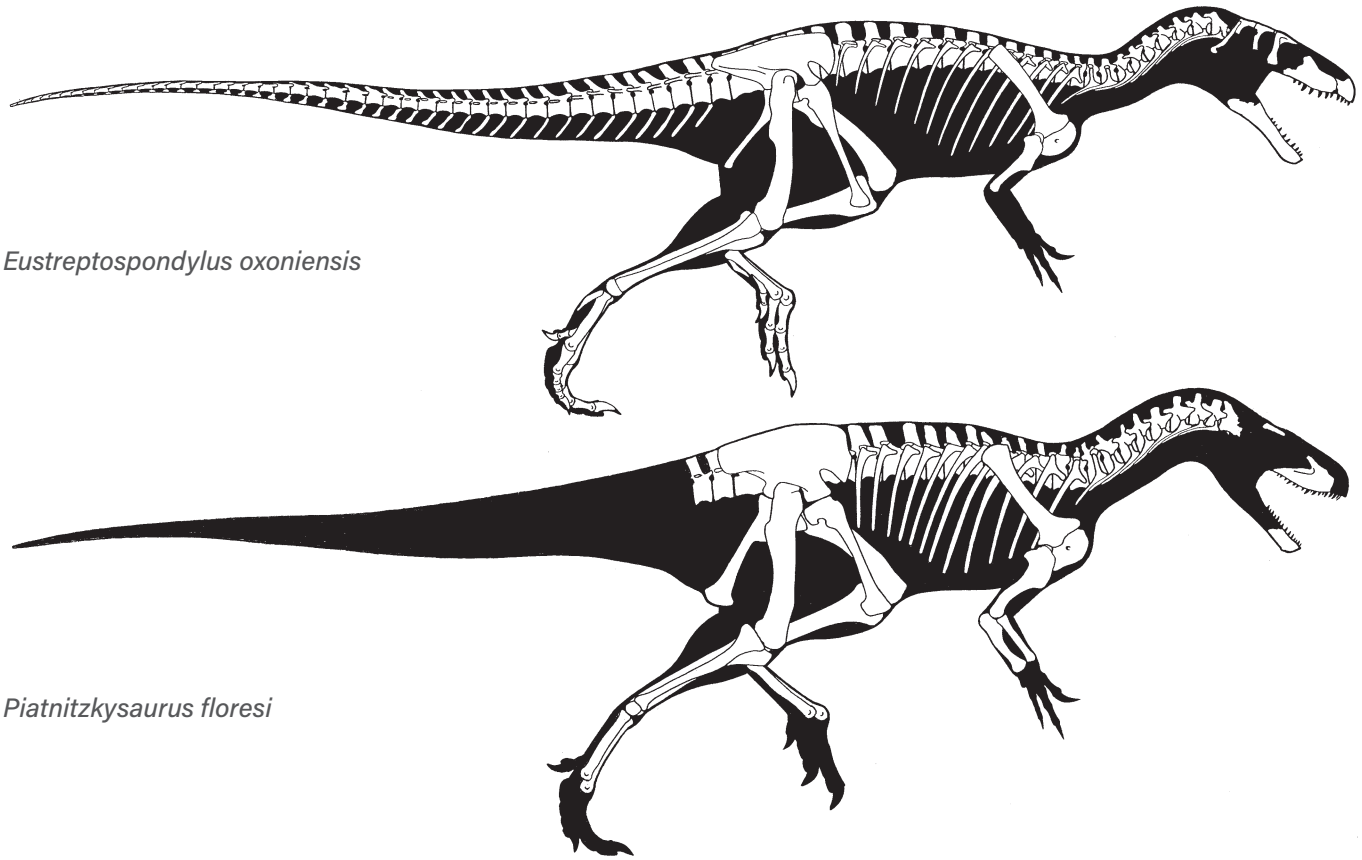
Chilesaurus diegosuarezi

— 2.5 m (8 ft) TL, 17 kg (35 lb)
FOSSIL REMAINS Partial skull and majority of skeletons.
ANATOMICAL CHARACTERISTICS Overall build slender. Head small, teeth leaf shaped, lightly serrated. Neck fairly long. Trunk elongated, pubis retroverted. Arm robust, third digit absent. Inner toes well developed, so foot almost tetradactyl.
AGE Late Jurassic, middle Tithonian.
DISTRIBUTION AND FORMATION/S Chile; Toqui.
HABITS Herbivorous or omnivorous.
NOTES Exact relationships with other avepods uncertain. Another example of avepods evolving herbivory, and of reenlarging the inner toe—almost as much as therizinosaurs and similar to *Balaur*—and another example of dinosaurs retroverting the pubis, in this case to enlarge the gut for herbivory. Fragmentary Asian Early Jurassic *Eshanosaurus deguchiianus* may be a relative.

— MEGALOSAUROIDS

LARGE TO VERY LARGE PREDATORY TETANURANS OF THE JURASSIC ON MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Heads large, low. Tails long.
NOTES The relationships of the following megalosauroids are uncertain. Absence from Australia and Antarctica probably reflects lack of sufficient sampling.

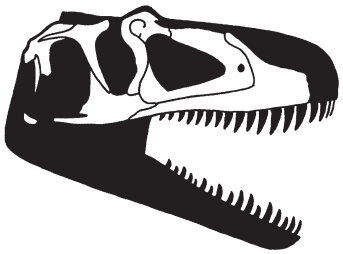


Eustreptospondylus oxoniensis

Piatnitzkysaurus floresi

Eustreptospondylus oxoniensis
— 4.5 m (15 ft) TL, 240 kg (500 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Lightly built. Teeth widely spaced.
AGE Middle Jurassic, late Callovian.
DISTRIBUTION AND FORMATION/S Southern England; middle Oxford Clay.

Marshosaurus bicentesimus
— 4.5 m (15 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, early and/or middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Utah; middle Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.



Afrovenator abakensis

Piatnitzkysaurus floresi
— 4.5 m (15 ft) TL, 300 kg (650 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Lightly built.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cañadón Asfalto.

Condorraptor currumili
— 4.5 m (15 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cañadón Asfalto.

Afrovenator abakensis
— 8 m (25 ft) TL, 1.5 tonne
FOSSIL REMAINS Majority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Lightly built. Orbital hornlet modest, teeth large. Leg long.
AGE Late Middle or early Late Jurassic.
DISTRIBUTION AND FORMATION/S Niger; Tiourarén.
HABITAT/S Well-watered woodlands.
HABITS Pursuit predator.

NOTES Originally thought to be from the Early Cretaceous; Tiourarén now placed in the later Jurassic. This, *Dubreuillosaurus*, and *Magnosaurus* may form subfamily Afrovenatorinae.

Dubreuillosaurus valesdunensis

Dubreuillosaurus valesdunensis

— 5 m (16 ft) TL, 350 kg (750 lb)
FOSSIL REMAINS Majority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Teeth large.
AGE Middle Jurassic, middle Bathonian.
DISTRIBUTION AND FORMATION/S Northwestern France; Calcaire de Caen.
HABITAT/S Coastal mangroves.
NOTES Not a species of *Poekilopleuron*, as originally thought.

Magnosaurus nethercombensis

— 4.5 m (15 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Aalenian or Bajocian.
DISTRIBUTION AND FORMATION/S Southwestern England; Inferior Oolite.

— MEGALOSAURIDS

VERY LARGE PREDATORY MEGALOSAUROIDS LIMITED TO THE MIDDLE AND LATE JURASSIC OF EUROPE AND NORTH AMERICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Massively constructed. Teeth stout. Lower arms short and stout. Pelves broad and shallow. Brains reptilian.
HABITAT/S Seasonally dry to well-watered woodlands.
HABITS Ambush predators.

Duriavenator hesperis

— 7 m (23 ft) TL, 1 tonne
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Teeth in lower jaw widely spaced.
AGE Middle Jurassic, late Bajocian.
DISTRIBUTION AND FORMATION/S Southern England; upper Inferior Oolite.

Megalosaurus bucklandii

— 6 m (20 ft) TL, 700 kg (1,600 lb)
FOSSIL REMAINS Lower jaw and possibly skeletal parts.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Middle Jurassic, middle Bathonian.
DISTRIBUTION AND FORMATION/S Central England; Stonesfield Slate.
NOTES Over the years *Megalosaurus* became a taxonomic grab bag into which a large number of remains from many places and times were placed. The genus and species may be limited to the original fossil, the full extent of which is not entirely certain.

Poekilopleuron? *bucklandii*

— 7 m (23 ft) TL, 1 tonne
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Appears to be standard for group.
AGE Middle Jurassic, middle Bathonian.
DISTRIBUTION AND FORMATION/S Northwestern France; Calcaire de Caen.
NOTES Because at least some bones of this and contemporary and nearby *Megalosaurus bucklandii* are very similar, it is possible that this is the same genus and even species as the latter, or some of the original remains placed in the British megalosaur may belong to this theropod. Original remains destroyed by Allied bombardment in World War II.

Torvosaurus tanneri

— 9 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of a skull and partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming, Utah; middle Morrison.

Torvosaurus tanneri

composite megalosaurid

HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Remains imply this genus or close relations were present in the lower Morrison and/or the later Portuguese lower and middle Lourinhã Formation; in the latter a nest with eggs and embryos may belong to that taxon.

— SPINOSAURS

LARGE TO GIGANTIC FISHING AND PREDATORY TETANURANS OF THE CRETACEOUS OF EURASIA, AFRICA, AND SOUTH AMERICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Long trunked. Heads very long and shallow; snouts elongated, narrow, and tips hooked; tips of lower jaws expanded, teeth conical; low central crest above orbits, lower jaws could bow outward. Tails long. Arms well developed, three fingers, claws large hooks. Legs short. Brains reptilian. Skeletons less pneumatic than usual for tetanurans.
HABITAT/S Large watercourses or coastlines.
HABITS Trophically flexible, being able to prey on large animals and also small game hunters with specializations for fishing using crocodilian-like heads and teeth, outward-bowing pelican-like mandibles, and hooked hand claws. Reduced pneumatic spaces indicate more adapted for swimming than other theropods, but were still too buoyant to deep swim and fish like crocodilians. Head crests for display within the species. Being less pneumatic than most avepods, diving ablity improved, but not as deep diving as heavy-boned, armored crocodilians.
NOTES Very large Moroccan snout represents largest known theropod at about 15 m (50 ft) long and 13 tonnes. Absence from at least some other continents may reflect lack of sufficient sampling.

Ichthyovenator laosensis
— 8.5 m (27 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Vertebral spines moderately tall and broad.
AGE Early Cretaceous, late Barremian or early Cenomanian.
DISTRIBUTION AND FORMATION/S Laos; Grès Supérieurs.

Baryonyx walkeri
— 7.5 m (25 ft) TL, 1.3 tonnes
FOSSIL REMAINS Partial skull and skeleton.

Baryonyx walkeri

ANATOMICAL CHARACTERISTICS Small central crest over orbits.
AGE Early Cretaceous, Barremian.
DISTRIBUTION AND FORMATION/S Southeastern England; Weald Clay.

Baryonyx (= *Suchomimus*) *tenerensis*

— 9.5 m (30 ft) TL, 3.1 tonnes
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Small central crest over orbits. Vertebral spines moderately tall.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Niger; upper Elrhaz.
HABITAT/S Coastal river delta.
NOTES Probably includes *Cristatusaurus lapparenti*.

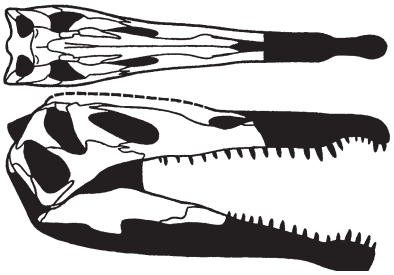
Irritator challengeri

— 7.5 m (25 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Long, low midline crest over back of head, back of head deep.
AGE Early Cretaceous, probably Albian.
DISTRIBUTION AND FORMATION/S Eastern Brazil; Santana.
NOTES Found as drift in nearshore marine sediments, a snout tip labeled *Angaturama limai* from same formation may belong to this species or even same fossil. There is evidence of predation on a pterosaur.

Spinosaurus aegyptiacus

— 11 m (35 ft) TL, 6 tonnes
FOSSIL REMAINS Uncertain.
ANATOMICAL CHARACTERISTICS Uncertain.
DISTRIBUTION AND FORMATION/S Egypt; Bahariya.
HABITAT/S Coastal mangroves.
NOTES Destroyed by Allied bombing during World War II, not certain if very incomplete original remains including very tall vertebral spines represent one or two types of theropods, the spines may be those of an allosauroid. Assignment of fossils from distant regions of Africa is too problematic to allow reliable restoration and assessment of function and habits. Reconstructions with very short legs and sails are problematic.

Baryonyx (=*Suchomimus*) *tenerensis*



Irritator challengeri

— AVETHEROPODS

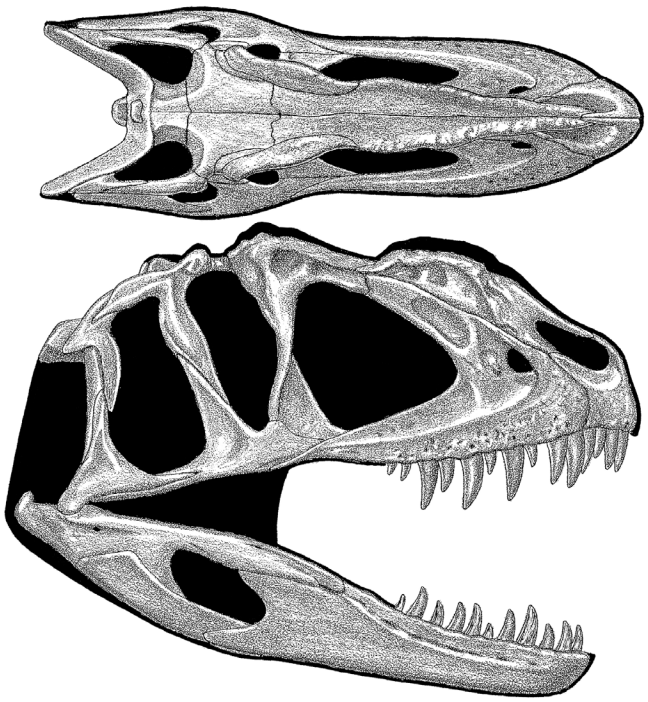
SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS TETANURANS FROM THE MIDDLE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Extra joint in lower jaws usually better developed. Arms very long to very reduced, enlarged semilunate inner carpal block for increased wrist flexion usually at least incipient. Birdlike respiratory system highly developed. Brains reptilian to avian.
NOTES Absence from Mesozoic Antarctica probably reflects lack of sufficient sampling.

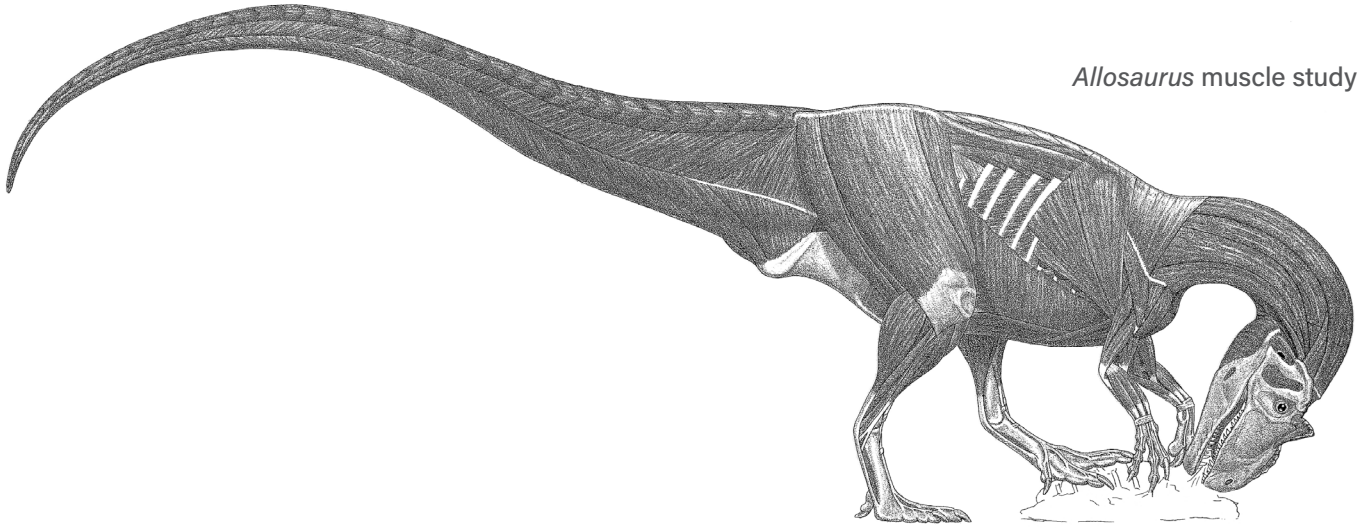
— ALLOSAUROIDS

LARGE TO GIGANTIC PREDATORY AVETHEROPODS FROM THE MIDDLE JURASSIC TO THE EARLY LATE CRETACEOUS, ON MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Moderately variable. Conventional avetheropod form, heads and trunks moderately robustly built and muscled. Heads generally subtriangular in side view, not very broad, preorbital hornlets modest to well developed, bladed teeth not very large. Tails long. Arm length medium to short. Legs moderately long. Brains reptilian.
HABITS Ambush and pursuit big game hunters. Heads and arms used as weapons. Extreme size of some species indicates that adults hunted adult as well as younger sauropods, armored ornithischians, and large ornithopods using heads and long tooth rows powered by powerful neck muscles to dispatch victims with slashing bites intended to cripple prey so it could be safely consumed. Arms used to handle and control prey when necessary.
NOTES Fragmentary remains imply presence in Australia. If megaraptorids are allosauroids rather than tyrannosaurids, as some research indicates, then this group survived until the end of the dinosaur era.
The standard big theropod type. Group has been labeled carnosaurs.



Yangchuanosaurus shaded skull



Allosaurus muscle study

— ALLOSAUROID MISCELLANEA

Asfaltovenator vialidadi

— 7 m (23 ft) TL, 1 tonne
FOSSIL REMAINS Skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout large and upper profile gently arced, snout ridges not well developed, rounded brow hornlet not prominent. Thumb robust. Pubic boot may not be large.
AGE Late Middle or early Late Jurassic.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cañadón Asfalto, level uncertain.

Asfaltovenator vialidadi

HABITAT/S Short wet season, otherwise semiarid with riverine forests and open floodplains.
NOTES May be most basal known allosauroid.

— YANGCHUANOSAURIDS

LARGE TO GIGANTIC ALLOSAUROIDS LIMITED TO THE MIDDLE AND LATE JURASSIC OF EURASIA.

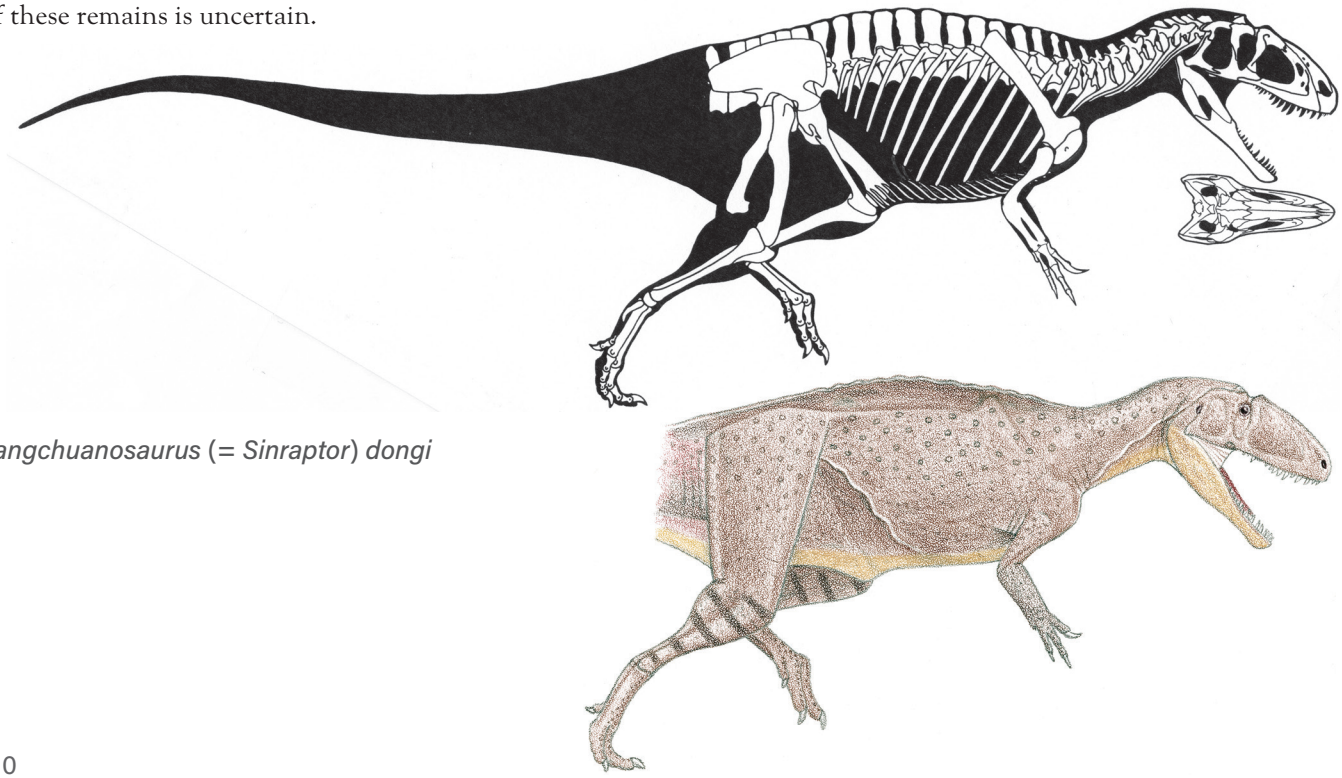
ANATOMICAL CHARACTERISTICS Uniform. Brow hornlets not prominent. Remnant of fourth finger present.
NOTES Relationships within group and naming of group are uncertain. Incomplete Asian, Middle Jurassic, juvenile *Gasosaurus constructus* and fragmentary European, Late Jurassic *Metriacanthosaurus parkeri* may belong to this group. Fragmentary *Siamotyrannus isanensis* may or may not indicate survival of the group into Early Cretaceous.

Yangchuanosaurus? *zigongensis*

— Adult size uncertain
FOSSIL REMAINS Minority of two skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
NOTES Originally placed in *Szechuanosaurus campi*, which is based on inadequate remains; the identity of these remains is uncertain.

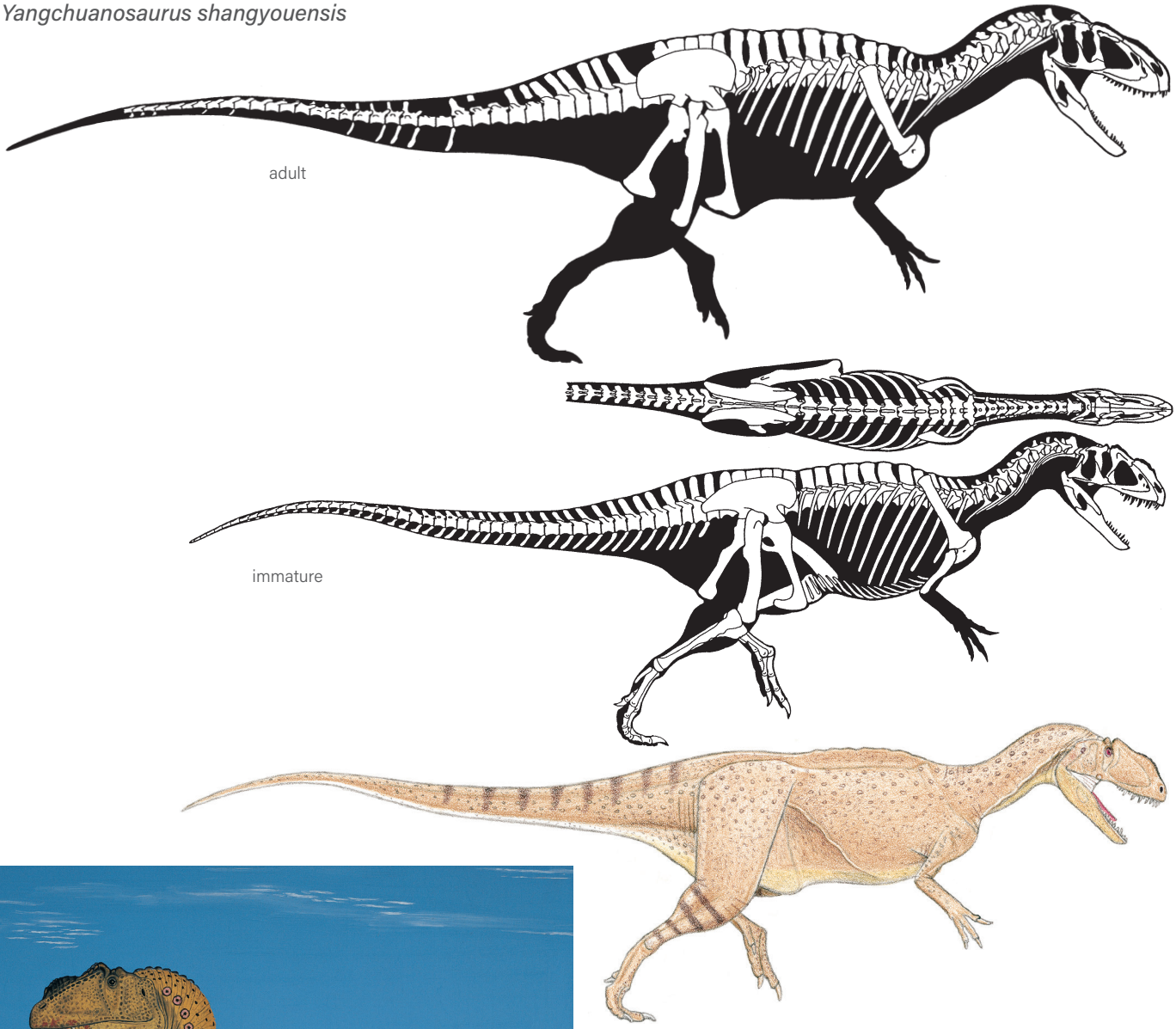
Yangchuanosaurus (= *Sinraptor*) *dongi*

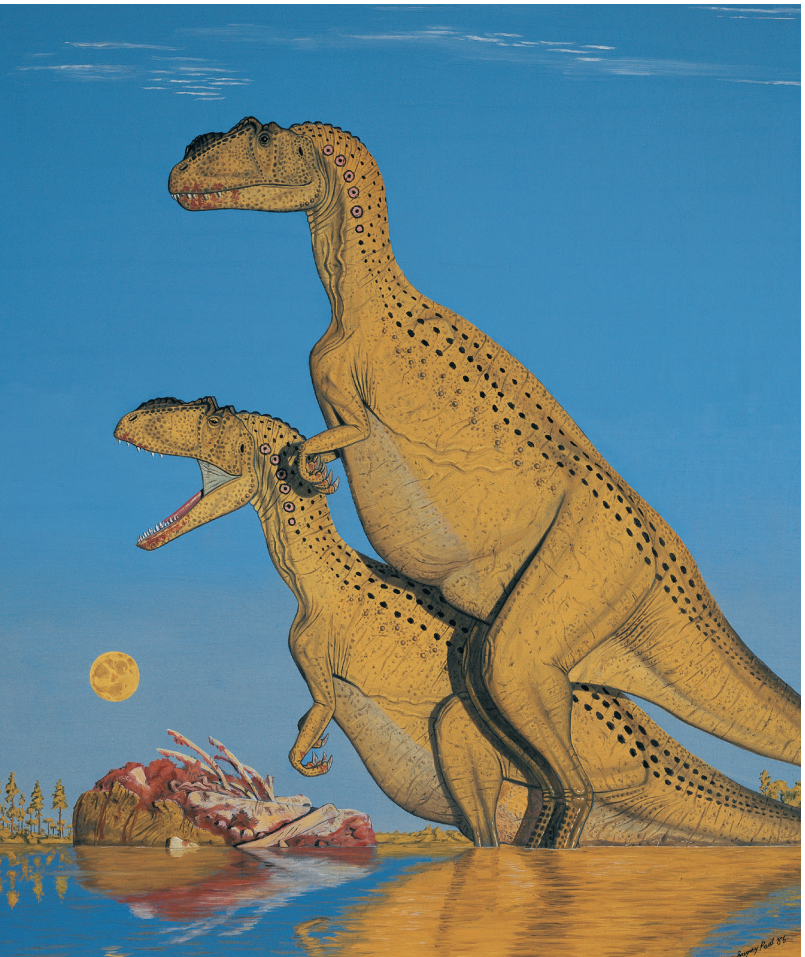
— 8 m (26 ft) TL, 1.5 tonnes
FOSSIL REMAINS Complete skulls and majority of a skeleton.
ANATOMICAL CHARACTERISTICS Snout ridges not well developed.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.
NOTES This species barely differs from *Y. shangyouensis*.



Yangchuanosaurus (= *Sinraptor*) *dongi*

Yangchuanosaurus shangyouensis





Yangchuanosaurus shangyouensis

— 11 m (35 ft) TL, 2.9 tonnes

FOSSIL REMAINS A few complete skulls and the majority of some skeletons, completely known.

ANATOMICAL CHARACTERISTICS Snout ridges well developed.

AGE Late Jurassic, probably Oxfordian.

DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.

HABITAT/S Heavily forested.

NOTES From the same formation, very similar and progressively larger in size, *Y. hepingensis*, *Y. shangyouensis*, and *Y. magnus* appear to form a progressive growth series within a single species. It is possible that the modest-sized, fairly complete but poorly described *Leshansaurus qianweiensis* from this formation may be a juvenile of this species, or it could be an afrovenator.

— ALLOSAURIDS

LARGE TO GIGANTIC ALLOSAUROIDS LIMITED TO THE LATE JURASSIC OF THE AMERICAS, EUROPE, AND AFRICA.

ANATOMICAL CHARACTERISTICS Uniform. Heads not especially large, back of head more rigidly braced; large, triangular, sharp-tipped brow hornlets present. Tails long. Boots of pubes large. Fourth finger entirely lost.
ONTOGENY Growth rates moderately rapid, adult size reached in about two decades; life spans normally not exceeding three decades.

Allosaurus jimmadseni

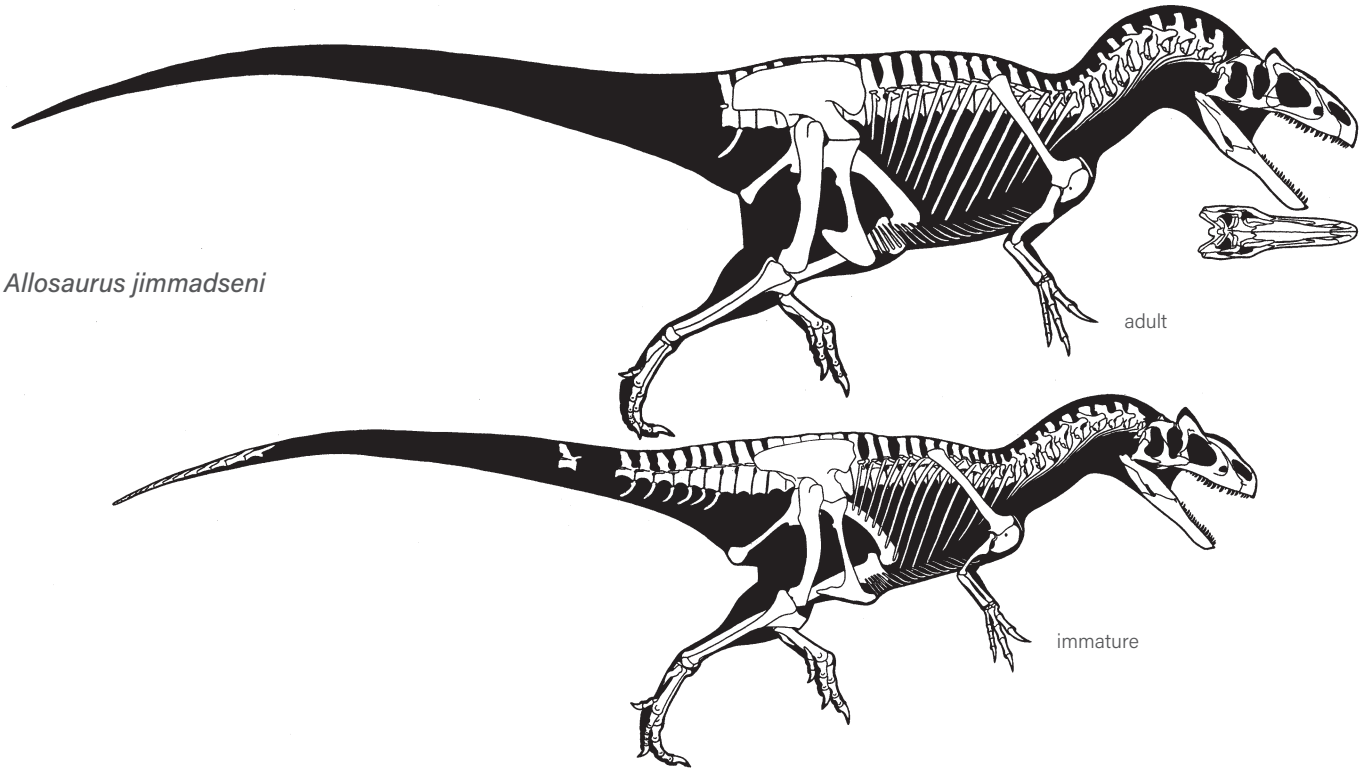
— Adult size uncertain
FOSSIL REMAINS Two skulls and skeletons, immature.
ANATOMICAL CHARACTERISTICS Head fairly elongated, narrow, temporal region not deep because edge of back of upper jaws is on same line as forward edge, nasal opening shallow, brow hornlet large. Arm and hand not large and/or slender.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Colorado, Utah; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Not as powerful a predator as later, more robust *A. fragilis*.

Allosaurus unnamed species?

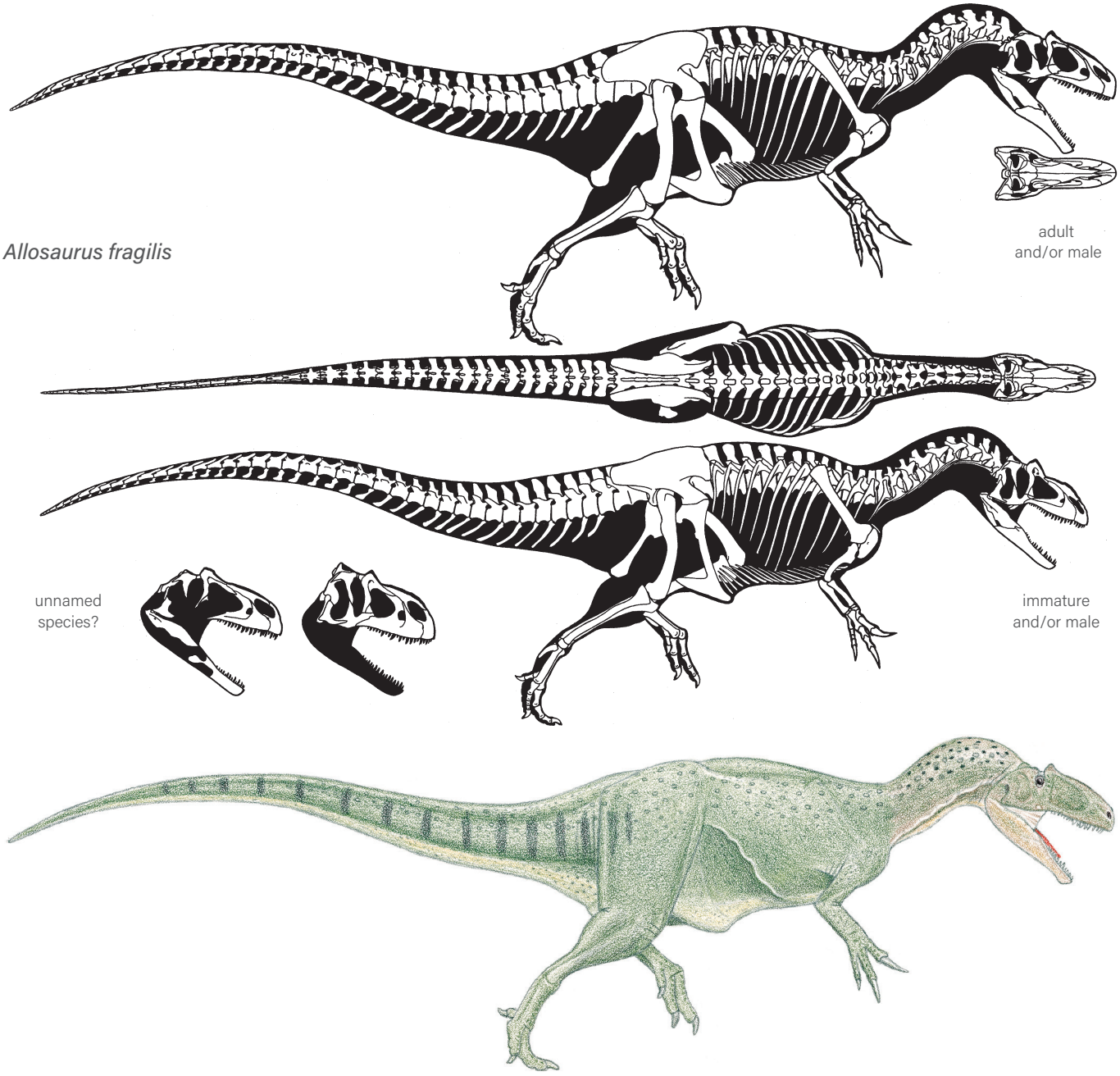
— 8.5 m (28 ft) TL, 1.7 tonnes
FOSSIL REMAINS Majority of two skulls.
ANATOMICAL CHARACTERISTICS Head fairly elongated, narrow, temporal region deep because edge of back of upper jaws is set down relative to forward edge, nasal opening deep, brow hornlet large. Arm and hand not large and/or slender.
AGE Late Jurassic, early Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; lower middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES May be a different species than later *A. fragilis*. Long versus short heads, found in same quarry, are probably genders, or contemporary species.

Allosaurus fragilis

— 8.5 m (28 ft) TL, 1.7 tonnes
FOSSIL REMAINS A large number of complete and partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head length/depth varies from moderately deep to deep, fairly broad, temporal region deep because edge of back of upper jaws is set down relative to forward edge, nasal opening shallow, brow hornlet large. Arm and hand large and stout.



Allosaurus jimmadseni



AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Utah, Wyoming, Colorado; upper middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES The classic nontyrannosaur large theropod. Heads are not similar in proportions, long versus short heads are probably genders, or contemporary species, includes *Antrodemus valens*, *Allosaurus lucasi* based on inadequate remains.

Saurophaganax (or *Allosaurus*) *maximus*

— 10.5 m (35 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of the skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Oklahoma; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Able to hunt larger sauropods.

Lourinhanosaurus antunesi and/or *Allosaurus*? *europaeus*

— Adult size uncertain

FOSSIL REMAINS Partial skull and skeletal remains, most or all immature and juvenile, possibly dozens of eggs with embryos.

ANATOMICAL CHARACTERISTICS Temporal region of skull deep because edge of back of upper jaws is set down relative to forward edge, nasal opening deep, brow hornlet large.

AGE Late Jurassic, early or middle Tithonian.

DISTRIBUTION AND FORMATION/S Portugal, middle Lourinhã.

HABITAT/S Large, seasonally dry island with open woodlands.

NOTES *L. antunesi* may be the juvenile of *A. europaeus*, which may not belong to same genus as much earlier *Allosaurus*.

— CARCHARODONTOSAURIDS

LARGE TO GIGANTIC ALLOSAUROIDS OF THE CRETACEOUS OF THE WESTERN HEMISPHERE, EURASIA, AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly variable. Boots of pubes further enlarged. Arms reduced.

HABITS Arms used less when hunting than in other allosauroids.

ONTOGENY Growth rates moderately rapid, adult size of larger examples reached in about three decades; life spans up to half a century.

NOTES Fragmentary Early Cretaceous *Datanglong guangxiensis* may indicate group's presence in Asia. Absence from additional continents may reflect lack of sufficient sampling.

Concavenator corcovatus

— 5 m (16 ft) TL, 330 kg (700 lb)

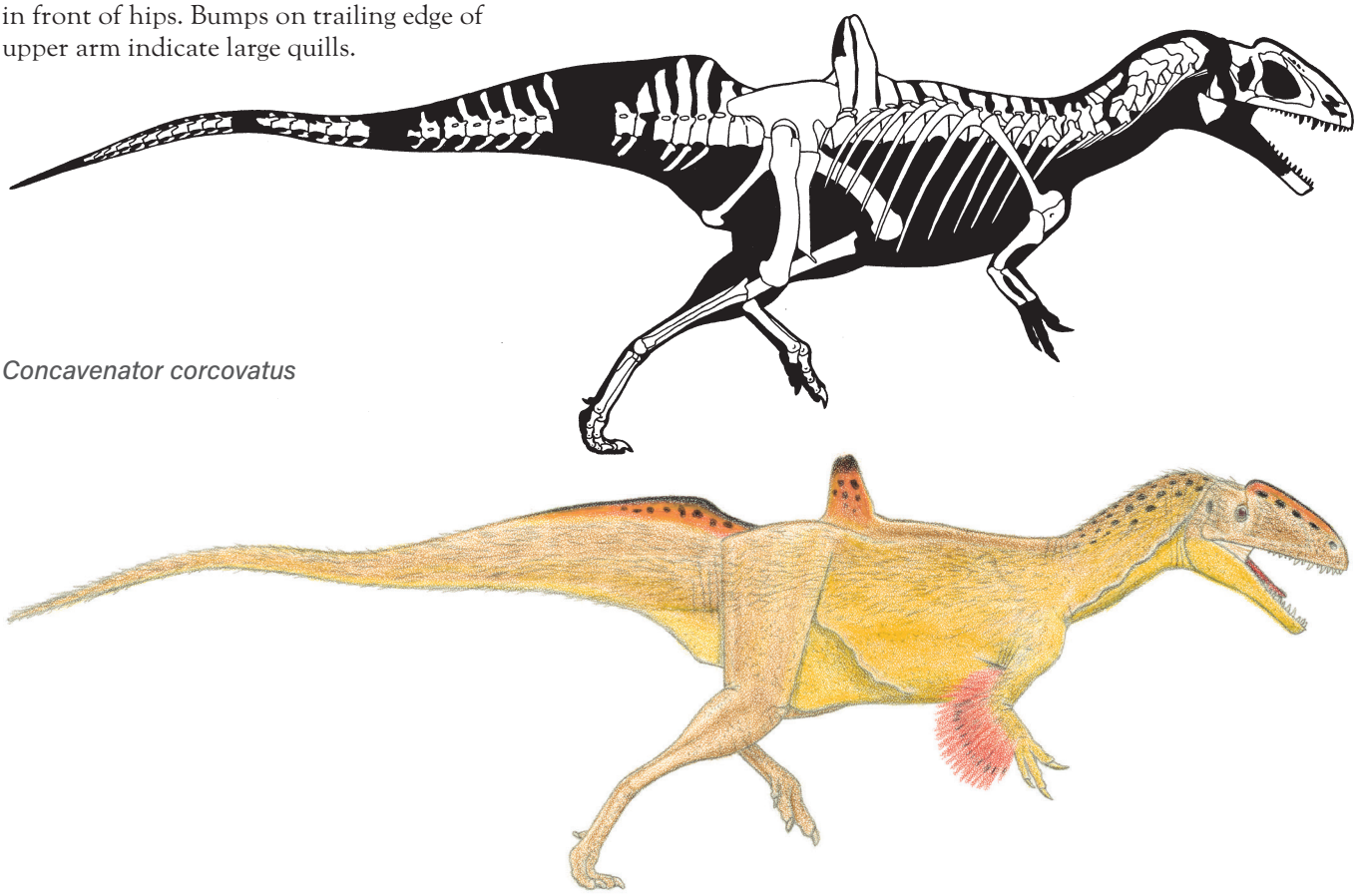
FOSSIL REMAINS Nearly complete skull and skeleton.

ANATOMICAL CHARACTERISTICS Brow hornlet well developed. Vertebral spines immediately in front of and behind pelvis tall, forming double sail back, especially in front of hips. Bumps on trailing edge of upper arm indicate large quills.

AGE Early Cretaceous, late Barremian.

DISTRIBUTION AND FORMATION/S Spain; Calizas de la Huérguina.

NOTES Possible quill nodes imply presence of feathery structures in allosauroids.



Concavenator corcovatus

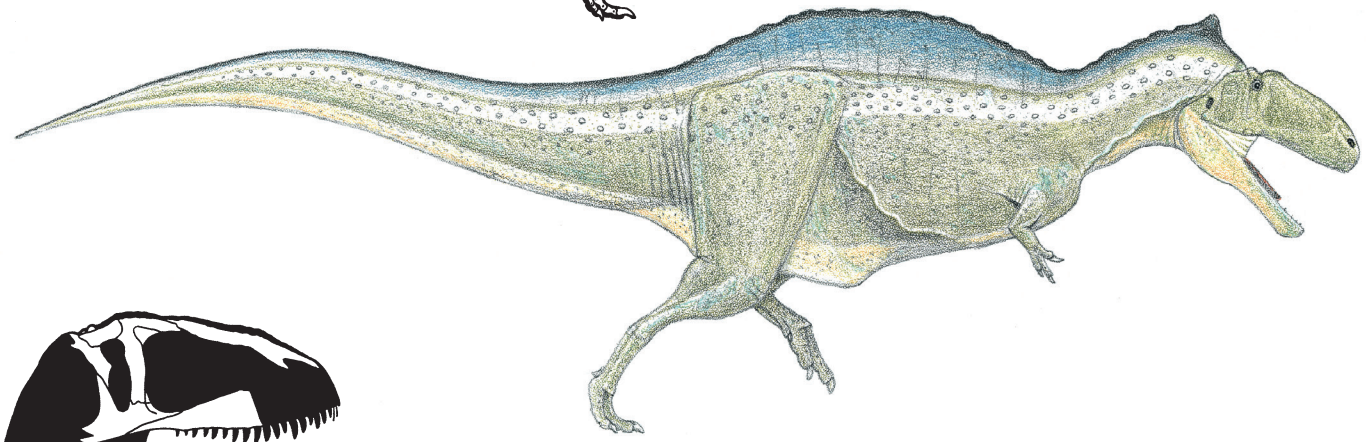
Acrocanthosaurus atokensis
— 11 m (35 ft) TL, 4.9 tonnes
FOSSIL REMAINS Complete skull and majority of skeletons.
ANATOMICAL CHARACTERISTICS Upper profile of snout gently arced, aft head markedly broader than snout, rounded brow hornlet not prominent, back of lower jaw deep. Tall vertebral spines from neck to tail form a low sail. Arm and hand moderately reduced.
AGE Early Cretaceous, Aptian or middle Albian.
DISTRIBUTION AND FORMATION/S Oklahoma, Texas; Antlers, level uncertain, Twin Mountains.
HABITAT/S Coastal floodplains with swamps and marshes.
NOTES Placement of all remains from many locations and uncertain spread of ages in same taxon is problematic. May be an allosaurid, a carcharodontosaurid, or its own group.

Eocarcharia dinops
— Adult size uncertain
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Niger; Elrhaz, level uncertain.
NOTES The one fossil may be a large juvenile.

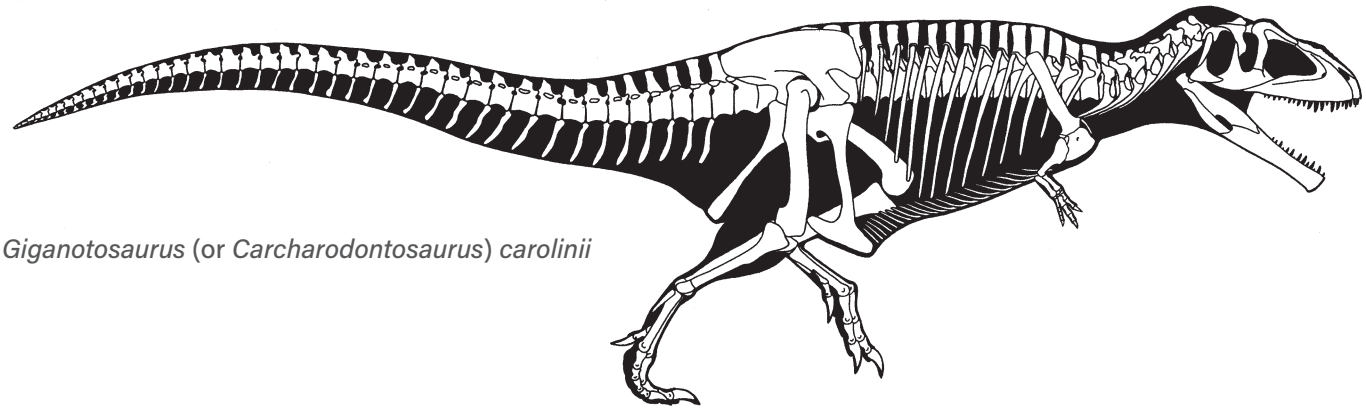
Tyrannotitan chubutensis
— 13 m (42 ft) TL, 9 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Vertebral spines over tail rather tall.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Southern Argentina; middle Cerro Barcino.
NOTES Among the largest avepods.

Carcharodontosaurus saharicus
— 12 m (40 ft) TL, 7 tonnes
FOSSIL REMAINS Partial skull and parts of skeletons.
ANATOMICAL CHARACTERISTICS Brow hornlet small.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Egypt, possibly Morocco and other parts of North Africa; Bahariya, upper Kem Kem Beds, etc.
HABITAT/S Coastal mangroves.

Acrocanthosaurus atokensis



Carcharodontosaurus saharicus



Giganotosaurus (or *Carcharodontosaurus*) *carolinii*

NOTES Whether remains from a large number of formations actually belong to this species is problematic.

Carcharodontosaurus iguidensis

— 10 m (34 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of several skulls and small portion of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Niger; Echkar.
NOTES Was placed in *C. saharicus*.

Giganotosaurus (or *Carcharodontosaurus*) *carolinii*

— 12.7–13.7 m (42–45 ft) TL, 8–10 tonnes
FOSSIL REMAINS Partial skull and majority of skeleton, minority of skull.
ANATOMICAL CHARACTERISTICS Brow hornlet not prominent. Front tip of lower jaw squared off.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
NOTES Partial carcharodontosaur skulls have been restored with too great a length. Arm in skeletal based on *Meraxes*. Size estimates complicated by incompleteness of largest known remains.

Meraxes gigas

Meraxes gigas

— 10 m (34 ft) TL, 4 tonnes
FOSSIL REMAINS Majority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Brow hornlet not prominent. Arm and hand moderately reduced. Inner main toe claw enlarged.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Mapusaurus roseae

— 11.5 m (38 ft) TL, 6 tonnes
FOSSIL REMAINS Large number of skull and skeletal bones.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, late Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; middle Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Shaochilong maortuensis

— 5 m (16 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Turonian.
DISTRIBUTION AND FORMATION/S Northern China; Ulansuhai.
NOTES Fossil may be a subadult.

— NEOVENATORIDS

LARGE TO GIGANTIC ALLOSAUROIDS OF THE CRETACEOUS OF EURASIA.

ANATOMICAL CHARACTERISTICS Fairly variable. Arms well developed.

Neovenator salerii

— 7 m (23 ft) TL, 1.3 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Lightly built, leg long. Head narrow.
AGE Early Cretaceous, early Barremian.
DISTRIBUTION AND FORMATION/S Southern England; lower Wessex.
NOTES That researchers have disagreed whether this is a basal tyrannosauroid or an allosauroid reinforces the two groups' close relationship.

Chilantaisaurus tashuikouensis

— 11 m (35 ft) TL, 5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Skeleton heavily constructed. Arm well developed.
AGE Late Cretaceous, Turonian.
DISTRIBUTION AND FORMATION/S Northern China; Ulansuhai.
NOTES The last of the known allosauroids, if this taxon belongs to this group.

— COELUROSAURS

SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS AVETHEROPODS OF THE MIDDLE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Tails long to very short. Arms from longer than legs to severely reduced. Legs extremely gracile to robust, toes four to three. Feathers often preserved.
HABITS Extremely variable, from big game predators to fully herbivorous.

— TYRANNOSAUROIDS

SMALL TO GIGANTIC PREDATORY AVETHEROPODS OF THE MIDDLE JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS EXCEPT ANTARCTICA.

ANATOMICAL CHARACTERISTICS Front teeth of upper jaw D-shaped in cross section. Arms long to severely reduced. Legs long. Brains reptilian.
HABITS Pursuit and ambush predators. Dispatched victims with powerful, deep, punch-like bites rather than slashing, wounding bites.
NOTES Proving to be long-lived and widely distributed. Although tyrannosauroids are not descended directly from allosauroids, the two groups may share a close common ancestor.

— BASO-TYRANNOSAUROIDS

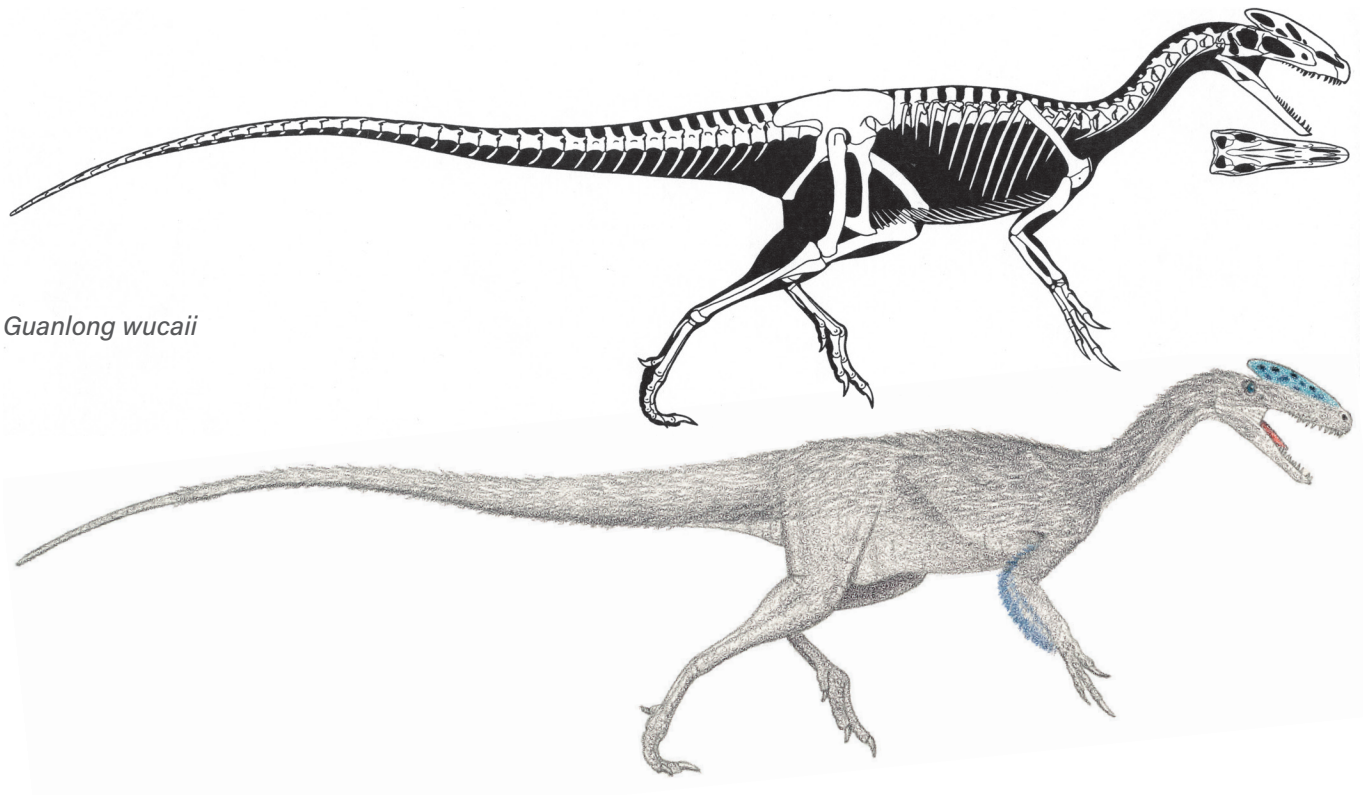
SMALL TO GIGANTIC TYRANNOSAUROIDS OF THE MIDDLE JURASSIC TO THE END OF THE DINOSAUR ERA.

ANATOMICAL CHARACTERISTICS Fairly variable. Arms not reduced. Legs not as gracile as those of tyrannosaurids.
HABITS Arms as well as head used to handle and wound prey.

Proceratosaurus bradleyi

— 3.5 m (11 ft) TL, 110 kg (250 lb)
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout fairly deep and adorned with nasal hornlet or crest, back of head rigidly built, teeth fairly large.
AGE Middle Jurassic, middle Bathonian.
DISTRIBUTION AND FORMATION/S Central England; Forest Marble.
HABITS Crest too delicate for headbutting; for display within the species.
NOTES Name incorrectly implies an ancestral relationship with the very different *Ceratosaurus*. This, *Guanlong*, *Sinotyrannus*, and *Juratyrant* may form family Proceratosauridae.

Proceratosaurus bradleyi



Guanlong wucaii

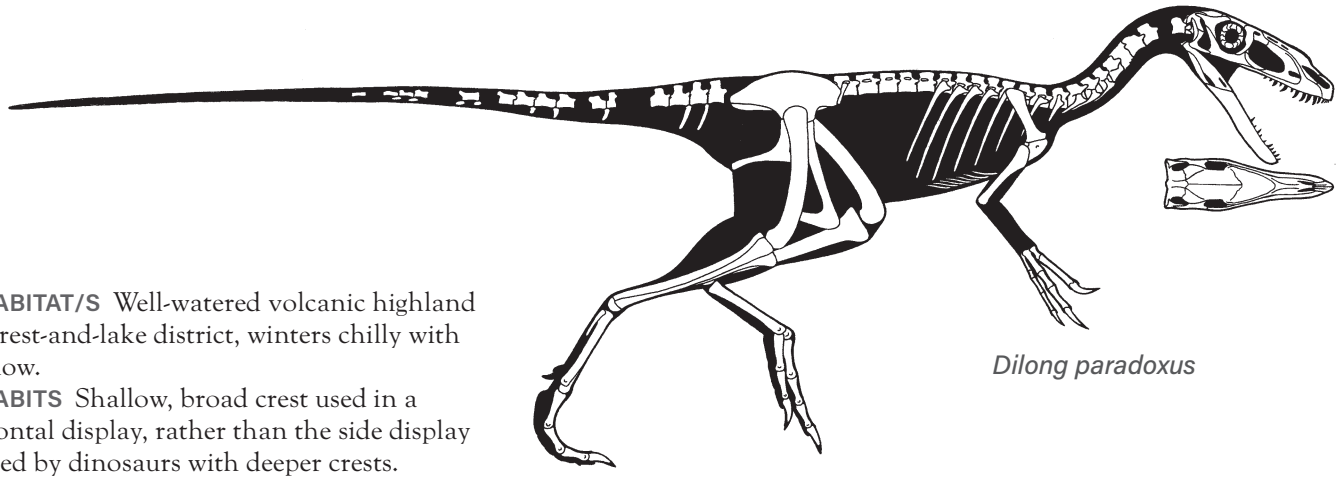
Guanlong wucaii
— 3.5 m (11 ft) TL, 110 kg (250 lb)
FOSSIL REMAINS Nearly complete skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout ridges united and enlarged into an enormous midline crest with a backward projection.
AGE Middle Jurassic, late Callovian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Shishugou.
HABITS Crest too delicate for headbutting, for display within the species.
NOTES Probably not as suggested a juvenile of *Monolophosaurus*.

Sinotyrannus kazuoensis
— 9 m (30 ft) TL, 2.5 tonnes
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Juratyrant langhami
— 5 m (16 ft) TL, 300 kg (600 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Lightly built.
AGE Late Jurassic, early Tithonian.
DISTRIBUTION AND FORMATION/S Southern England; Kimmeridge Clay.
NOTES Originally placed in the smaller baso-tyrannosaurid *Stokesosaurus*, the original species of which, *S. clevelandi* from the Late Jurassic of western North America, is based on one bone.

Aviatyrannis jurassica
— 1 m (3 ft) TL, 4 kg (10 lb)
FOSSIL REMAINS Small portion of skeleton, possibly juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Portugal; Camadas de Alcobaça.
HABITAT/S Large, seasonally dry island with open woodlands.

Dilong paradoxus
— Adult size uncertain
FOSSIL REMAINS A few nearly complete skulls and partial skeletons, external fibers, possibly juvenile.
ANATOMICAL CHARACTERISTICS Head long and low, low Y-shaped crest on snout. Hand fairly long. Leg very long. Full extent of protofeather covering uncertain.
AGE Early Cretaceous, latest Barremian and earliest Aptian?
DISTRIBUTION AND FORMATION/S Northeastern China; lower and middle? Yixian.



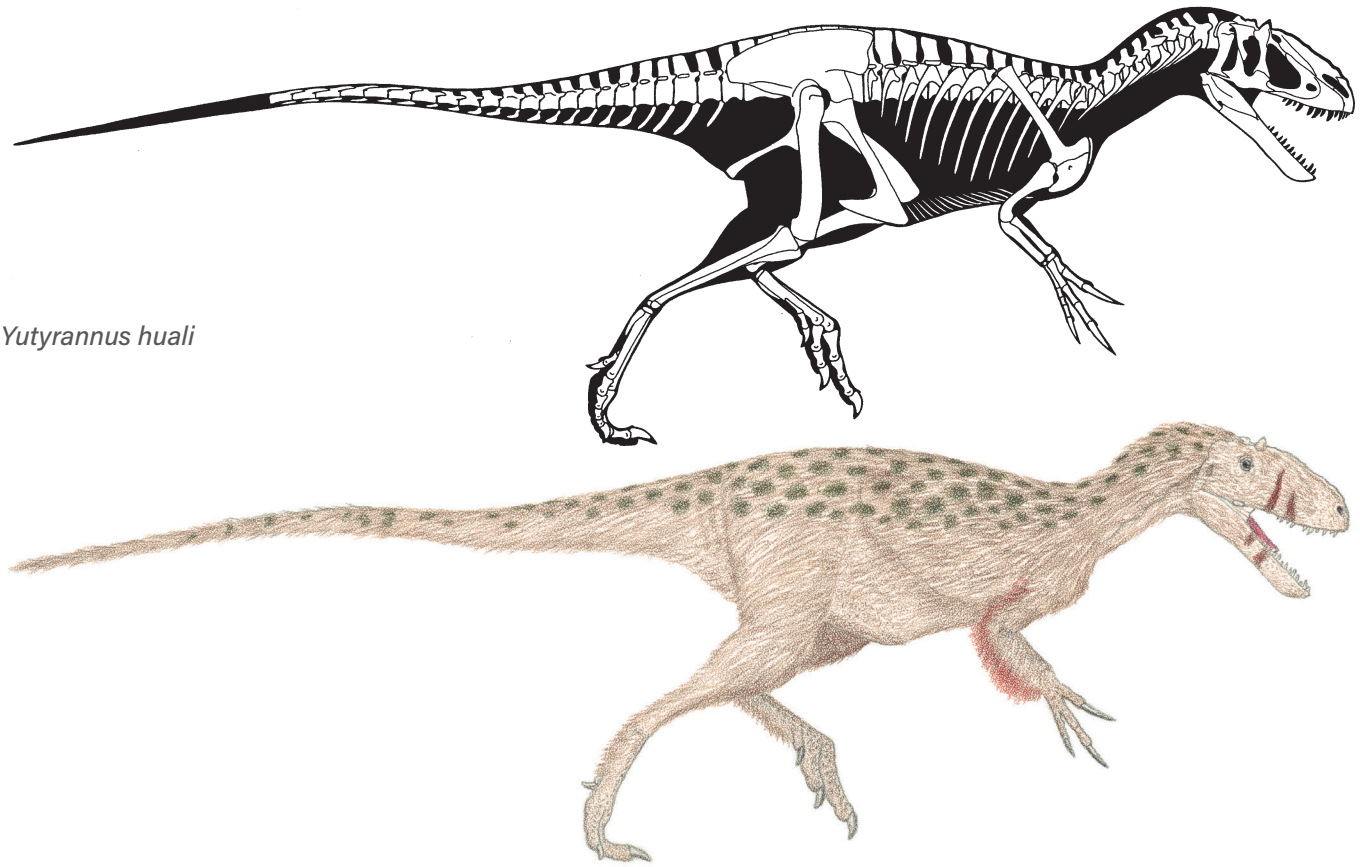
Dilong paradoxus

HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Shallow, broad crest used in a frontal display, rather than the side display used by dinosaurs with deeper crests.

Yutyrannus huali

— 7.5 m (25 ft) TL, 1.3 tonnes
FOSSIL REMAINS Three largely complete skulls and skeletons, two juvenile, external fibers.
ANATOMICAL CHARACTERISTICS Fairly robustly built. Snout fairly deep, large midline prominence atop back of head. Arm long. External fibers apparently covered much of body including upper foot.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian, level uncertain.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Yutyrannus huali



Yutyrannus huali

Eotyrannus lengi
— 3 m (10 ft) TL, 70 kg (150 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head strongly built, front of head deep. Skeleton lightly built. Arm long. Leg long and gracile.
AGE Early Cretaceous, early Barremian.
DISTRIBUTION AND FORMATION/S Southern England; lower Wessex.

Bagaraatan ostromi
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton, immature.
ANATOMICAL CHARACTERISTICS Lightly constructed. Tail stiffened.
AGE Late Cretaceous, late Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

Fukuiraptor kitadaniensis
— 5 m (16 ft) TL, 300 kg (600 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Lightly built, leg long.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Central Japan; Kitadani.

Australovenator wintonensis
— 6 m (20 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Lightly built, leg long.
AGE Early Cretaceous, late Cenomanian and/or early Turonian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; upper Winton.
HABITAT/S Well-watered, cold winters with heavy snows.

Megaraptor namunhuaiquii
— 8 m (25 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Hand claws slender.
AGE Late Cretaceous, late Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.
HABITAT/S Well-watered woodlands with short dry season.
NOTES Incorrectly thought to be the biggest dromaeosaurid; others consider this a spinosaur or an allosauroid. This, *Fukuiraptor*, *Australovenator*, *Aerosteon*, and *Orkoraptor* may form family Megaraptoridae.

Aerosteon riocoloradensis
— 6 m (20 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Lightly built, leg long.
AGE Late Cretaceous, late Santonian and/or early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; Anacleto.
HABITAT/S Seasonally semiarid.

Orkoraptor burkei
— 6 m (20 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Pari Aike.
NOTES If megaraptorids were allosauroids, as some researchers indicate, then *Orkoraptor* indicates that allosauroids lasted until close to and probably to the end of the dinosaur era.

Santanaraptor placidus
— 1.5 m (5 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, probably Albian.
DISTRIBUTION AND FORMATION/S Eastern Brazil; Santana.
NOTES Found as drift in nearshore marine sediments.

Xiongguanlong baimoensis
— 5 m (15 ft) TL, 200 kg (450 lb)
FOSSIL REMAINS Majority of a distorted skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head and especially snout long, low.
AGE Early Cretaceous, probably Aptian or Albian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.
HABITS Assuming the known fossils are adults, pursued similar-sized dinosaurs including ornithomimids.
NOTES Shows that some tyrannosauroids were fairly large in the mid-Cretaceous.

Labocania anomala
— 7 m (23 ft) TL, 1.5 tonnes
FOSSIL REMAINS Small portion of skull and skeleton.
ANATOMICAL CHARACTERISTICS Massively constructed.
AGE Late Cretaceous, probably Campanian.
DISTRIBUTION AND FORMATION/S Baja California, Mexico; La Bocana Roja.
HABITS Ambush big game hunter.

Appalachiosaurus? *montgomeriensis*
— Adult size uncertain
FOSSIL REMAINS Partial skull, skeleton.
ANATOMICAL CHARACTERISTICS Typically gracile for smaller tyrannosaurids.
AGE Late Cretaceous, early Campanian.
DISTRIBUTION AND FORMATION/S Alabama; Demopolis.
NOTES Found as drift in nearshore marine sediments. May have had fairly large arms. May be same genus as *Dryptosaurus*.

Dryptosaurus aquilunguis
— 7.5 m (25 ft) TL, 1.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Arm and especially hand large.
AGE Late Cretaceous, late Campanian or early Maastrichtian.
DISTRIBUTION AND FORMATION/S New Jersey; New Egypt.
HABITS Arms used as weapons.
NOTES Found as drift in nearshore marine sediments. May be a tyrannosaurid.

— TYRANNOSAURIDS

LARGE TO GIGANTIC TYRANNOSAUROIDS, LIMITED TO THE LATER LATE CRETACEOUS OF NORTH AMERICA AND ASIA.

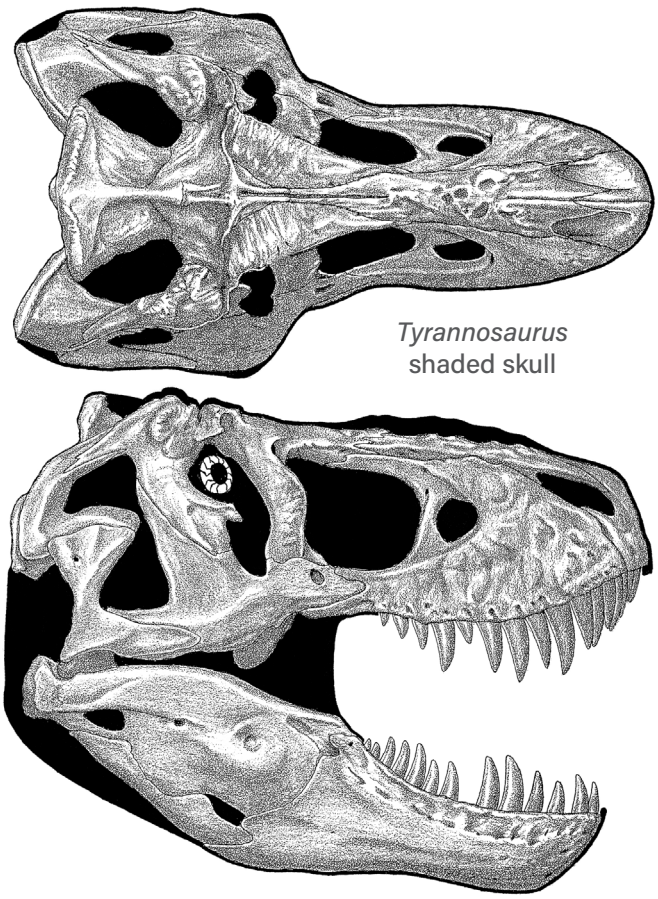
ANATOMICAL CHARACTERISTICS Fairly uniform, but juveniles and smaller species gracile, large adults more robust. Heads large and long, robustly constructed, stout bars in the temporal region invade the side openings and further strengthen the skull, skulls of juveniles and smaller species very long, shallow, and graceful, those of adults deeper and shorter snouted, midline ridge on snout rugose, probably bore long, possibly low ridge boss, small brow hornlets or bosses over orbits, usually small midline prominence atop back of head, back half of head a broad box accommodating exceptionally powerful jaw muscles, eyes face partly forward, and some degree of stereo vision possible, front of snout broader and more rounded than usual, supporting a U-shaped arc of teeth that are D-shaped in cross section, teeth stouter and more conical than in general, lower jaw deep, especially back half. Necks strongly constructed, powerfully muscled. Trunks short and deep. Tails shorter and lighter than standard in other large theropods. Arms severely reduced in size, outer fingers severely reduced to only two developed fingers, yet hands still functional. Pelves very large and legs very long, so leg muscles exceptionally well developed, feet very long and strongly compressed from side

to side. Reduction of tails and arms in favor of enlarged and elongated legs indicates greater speed potential than in other giant theropods. Scales small and pebbly, may have been mixed with fibers, which if present may have been limited to top surfaces. Skeletons of juveniles very gracile, becoming increasingly robust as size increases, but basic characteristics unaltered. Brains larger than usual in large theropods, olfactory bulbs especially large.

ONTOGENY Growth rates moderately rapid, adult size reached in about two decades; life span normally not exceeding three decades. Some small species that have been named are the juveniles of giant taxa; whether any species were small as adults is uncertain.

HABITS Pursuit and perhaps ambush predators; able to chase running prey at unusually high speeds. Compact form also enhanced maneuverability. Head the primary if not sole weapon. Long snouts of juveniles imply they were independent hunters. Giant adults used massive heads and strong teeth to dispatch victims with powerful, deep, punch-like bites rather than slashing, wounding bites aimed with forward vision, powered by very strong jaw and neck muscles, and intended to cripple prey so it could be safely consumed. Function of arms if any poorly understood; they appear too short and small to be useful in handling prey, may have provided grip for males while mating. Head bosses presumably for headbutting during intraspecific contests.

NOTES Overall the most advanced and sophisticated of large theropods. Large numbers of hunting juveniles may have swamped their habitats, suppressing the populations of smaller theropods such as dromaeosaurids and troodontids.



Tyrannosaurus shaded skull

Alectrosaurus olseni

— Adult size uncertain

FOSSIL REMAINS Partial skull, skeleton, possibly immature.

ANATOMICAL CHARACTERISTICS Typically gracile for smaller tyrannosaurids.

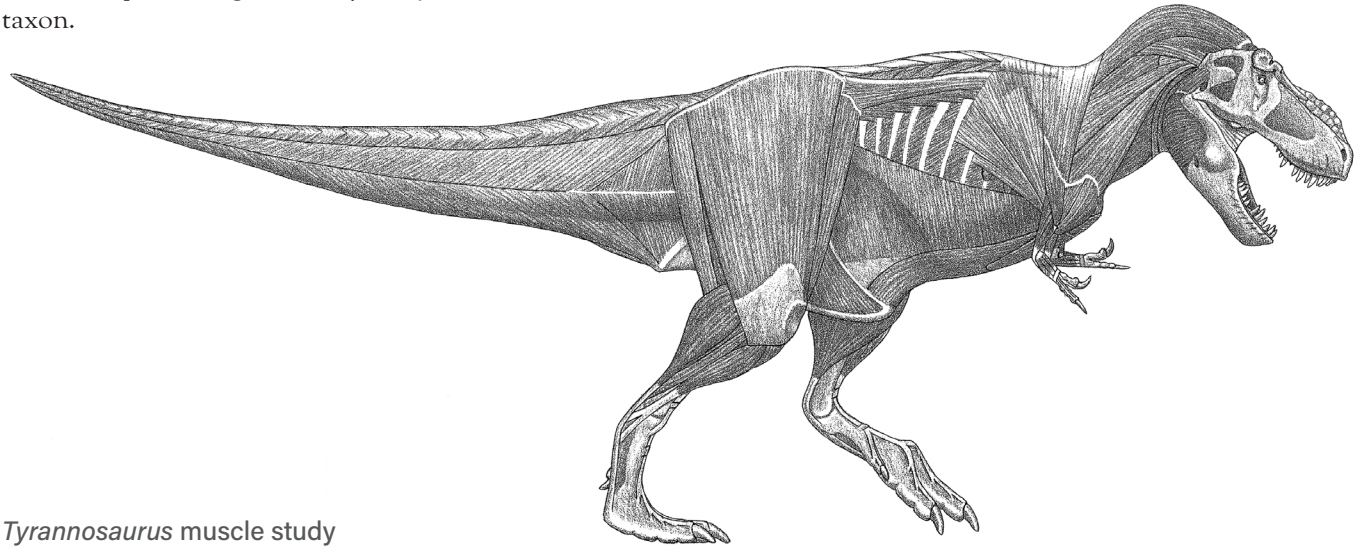
AGE Late Cretaceous.

DISTRIBUTION AND FORMATION/S China; Iren Dabasu.

HABITAT/S Seasonally wet-dry woodlands.

HABITS Assuming the known fossils are adults, pursued similar-sized dinosaurs including ornithomimids.

NOTES *Raptorex kriegstensis* may be a juvenile of this taxon.



Tyrannosaurus muscle study

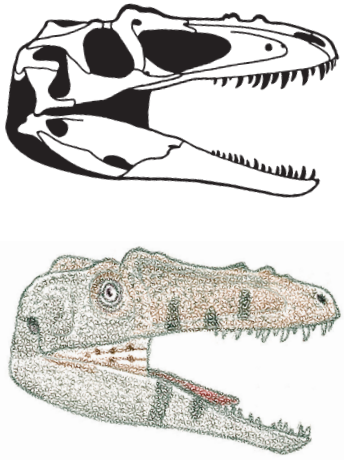
Alioramus remotus
— Adult size uncertain
FOSSIL REMAINS Skull, some parts of skeleton, possibly immature.
ANATOMICAL CHARACTERISTICS Typically gracile for smaller tyrannosaurids. Crenulated midline crest on snout.
AGE Late Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Nogoon Tsav.
HABITS Assuming the known fossils are adults, pursued similar-sized dinosaurs including ornithomimids.
NOTES This and *Qianzhousaurus* form subfamily Alioramini.

Alioramus altai
— Adult size uncertain
FOSSIL REMAINS Immature skulls, some parts of skeleton.
ANATOMICAL CHARACTERISTICS Head unusually long and low even for a tyrannosaur of this size. Crenulated midline crest on snout.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; Nemegt, level not available.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
HABITS Assuming the known fossils are adults, pursued similar-sized dinosaurs including ornithomimids.
NOTES Thought to be somewhat different in time from *A. remotus*; if not, may be the same species. *Raptorex kriegstensis* may be a juvenile of this genus. Competed with juvenile *Tyrannosaurus* (*Tarbosaurus*) *bataar*.

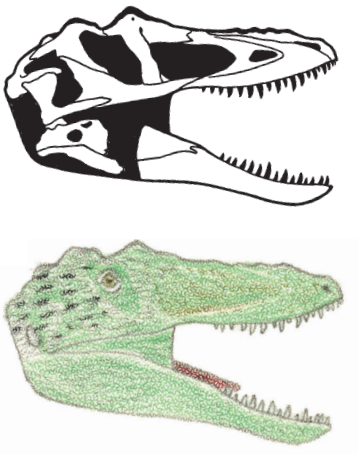
Alioramus (or *Qianzhousaurus*) *sinensis*
— Adult size uncertain
FOSSIL REMAINS Nearly complete skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Snout unusually slender even for a tyrannosaur of this size.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern China; Yuanpu.

Albertosaurus (*Gorgosaurus*) *libratus* (see p.124)
— 8 m (27 ft) TL, 2.7 tonnes
FOSSIL REMAINS A number of skulls and skeletons, adult and juvenile, small skin patches, completely known.
ANATOMICAL CHARACTERISTICS Brow hornlets fairly prominent. Skeleton not heavily built.
AGE Late Cretaceous, late middle? and/or early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta, Montana?; at least middle Dinosaur Park, upper Judith River?, upper Two Medicine?
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters, uplands drier.
HABITS Relatively gracile build indicates adults specialized in hunting unarmed hadrosaurs, although ceratopsians and ankylosaurs were probably occasional victims.
NOTES Often a separate genus, very similar to *Albertosaurus sarcophagus*. Differences including robustness of head may indicate different genders and/or species, remains from Montana may be latter, whether species lived through the entire time span of Dinosaur Park Formation also uncertain. May be direct ancestor of *A. sarcophagus*.

Albertosaurus (*Albertosaurus*) *sarcophagus*
— 8 m (27 ft) TL, 2.9 tonnes
FOSSIL REMAINS Some skulls and partial skeletons, adult and juvenile, well known.
ANATOMICAL CHARACTERISTICS Very similar to *A. libratus*. Leg may have been somewhat longer.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta, Montana; lower to middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

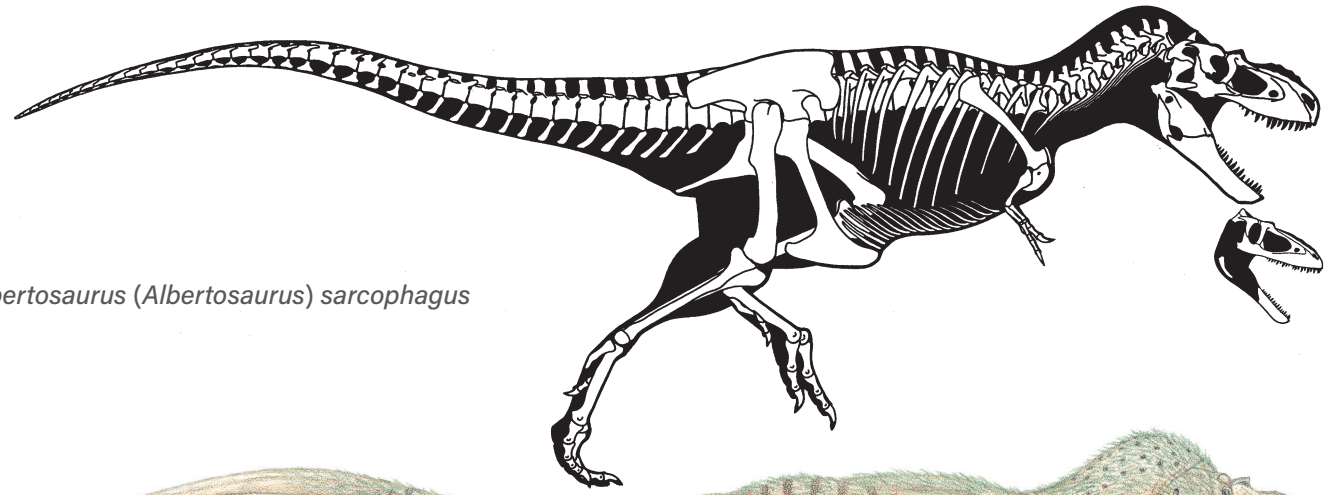


Alioramus remotus



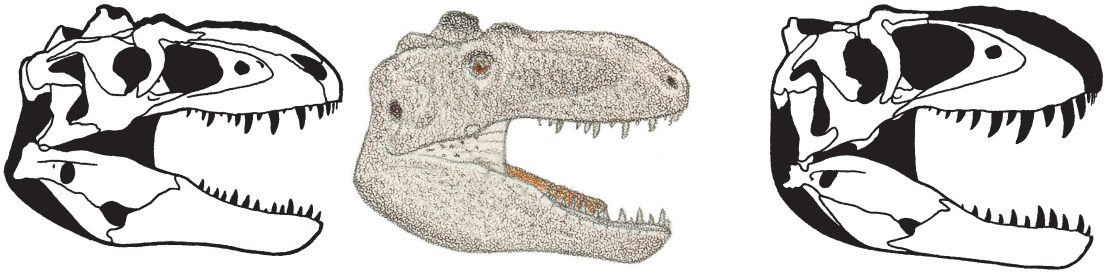
Alioramus (or *Qianzhousaurus*) *sinensis*

Albertosaurus (*Gorgosaurus*) *libratus* growth series



Albertosaurus (*Albertosaurus*) *sarcophagus*

Bistahieversor sealeyi



Teratophoneus curriei

HABITS Relatively gracile build indicates this species also preyed mainly on hadrosaurs.
NOTES Includes *A. arctunguis*, fossils from upper Horseshoe Canyon may be distinct taxon.

Lythronax argestes

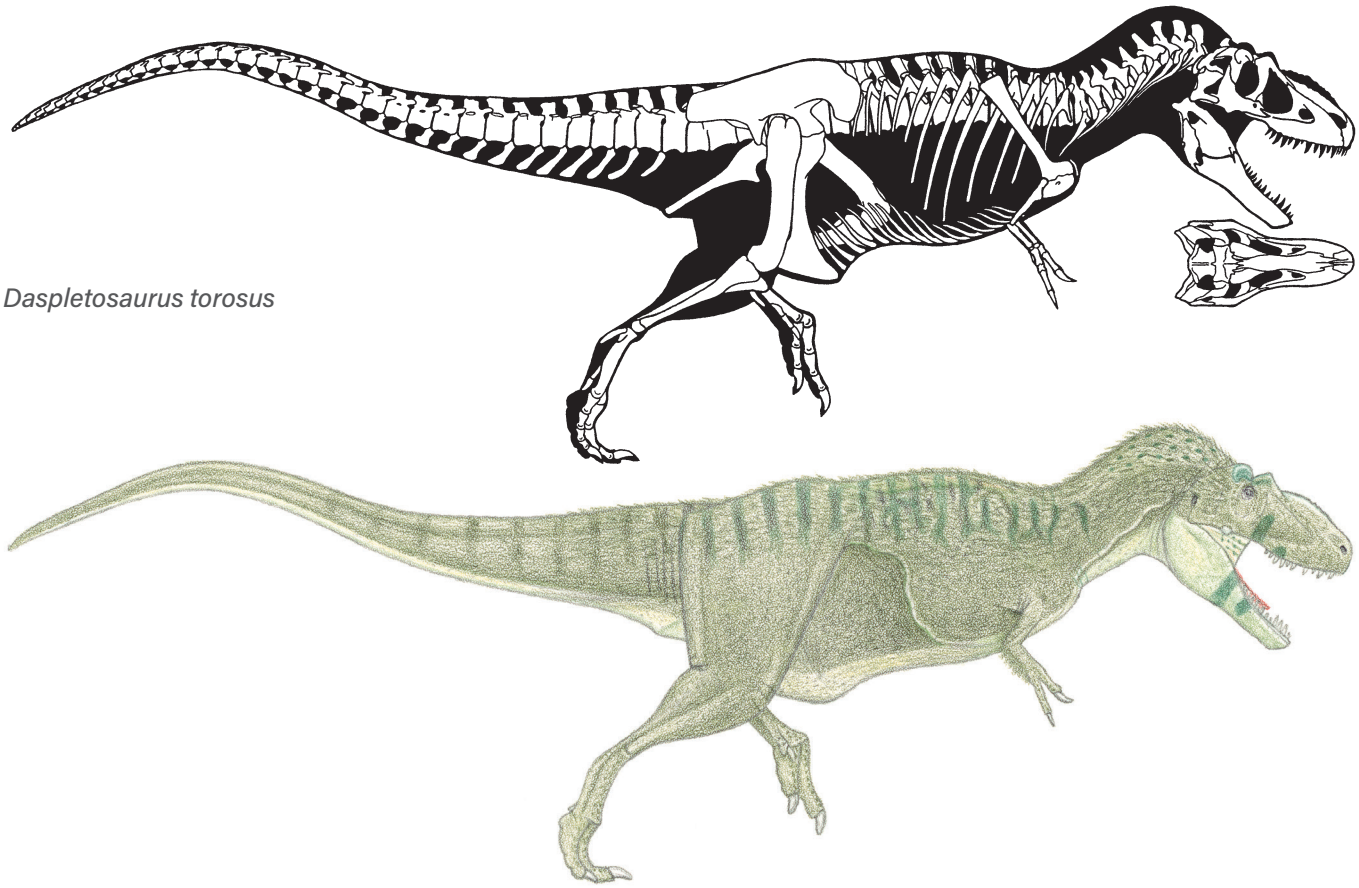
— 6.5 m (20 ft) TL, 1.5 tonnes
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Southern Utah; Wahweap.
NOTES Restoration of back of incomplete skull as exceptionally broad problematic.

Bistahieversor sealeyi

— 8 m (27 ft) TL, 2.5 tonnes
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Snout fairly deep, quite large midline prominence atop back of head.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; lower Kirtland.
NOTES May be a member of *Tyrannosaurus*. Information on skeleton insufficient for restoration.

Teratophoneus curriei

— 8 m (27 ft) TL, 2.5 tonnes
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Small triangular hornlet above orbit, modest supraorbital boss half moon shaped.



Daspletosaurus torosus

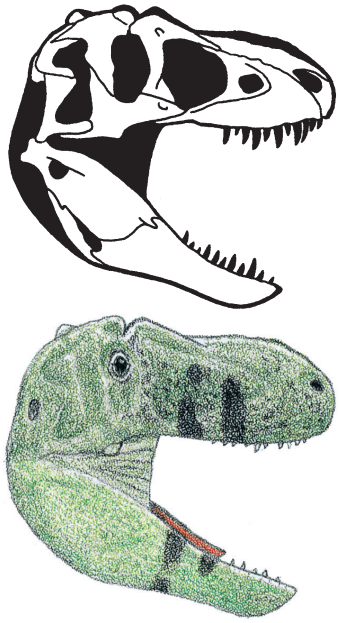
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Utah; middle Kaiparowits.
HABITS Tremendous strength of head indicates specialized for hunting horned ceratopsids.
NOTES There is some uncertainty about adult size. Extreme broadening of back of head similar to *Tyrannosaurus*, may be ancestral to latter.

Daspletosaurus torosus

— 9 m (30 ft) TL, 2.8 tonnes
FOSSIL REMAINS Complete skulls and majority of skeleton, other remains including juveniles.
ANATOMICAL CHARACTERISTICS Head broad, strongly constructed, supraorbital boss knob shaped, not highly prominent, teeth robust. Skeleton robustly built. Leg shorter than usual for group.
AGE Late Cretaceous, middle middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Oldman.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Stout build indicates this genus was specialized to cope with horned ceratopsids, and armored ankylosaurs when available, expanding the resource base it could prey on, although more vulnerable hadrosaurs were probably still common prey.
NOTES May be more than one species, may be direct ancestor of *D. wilsoni*.

Daspletosaurus wilsoni

— 9 m (30 ft) TL, 2.5 tonnes
FOSSIL REMAINS Some skulls and skeletons of varying completeness including juveniles.



Daspletosaurus wilsoni

ANATOMICAL CHARACTERISTICS Similar to *D. torosus* except head shallower, tip of snout rounded.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Montana, Alberta?; middle Judith River, lower Dinosaur Park?
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be direct ancestor of *D. horneri*.

Daspletosaurus horneri

— 9 m (30 ft) TL, 2.5 tonnes
FOSSIL REMAINS Two or three skulls and partial remains, juvenile to adult.
ANATOMICAL CHARACTERISTICS Similar to *D. torosus*.
AGE Late Cretaceous, early late Campanian.
DISTRIBUTION AND FORMATION/S Montana, Alberta?; upper Two Medicine, middle Dinosaur Park?
HABITAT/S Seasonally dry upland woodlands.
NOTES Modest time separation suggests two Montana skulls may be different geotime species, a Dinosaur Park skull may be same species. Daspletosaurs may be ancestral to *Tyrannosaurus* and its Asian relations.

Daspletosaurus? unnamed species

— 11 m (36 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Robust. Large brow hornlet.
AGE Late Cretaceous, middle Campanian.

Daspletosaurus horneri

DISTRIBUTION AND FORMATION/S Montana; lower Judith River.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Originally thought to be *Tyrannosaurus* from lower Hell Creek. If revised age is correct, indicates that western North American tyrannosaurids approached *Tyrannosaurus* size much earlier than thought, albeit not commonly. May be a distinct genus.

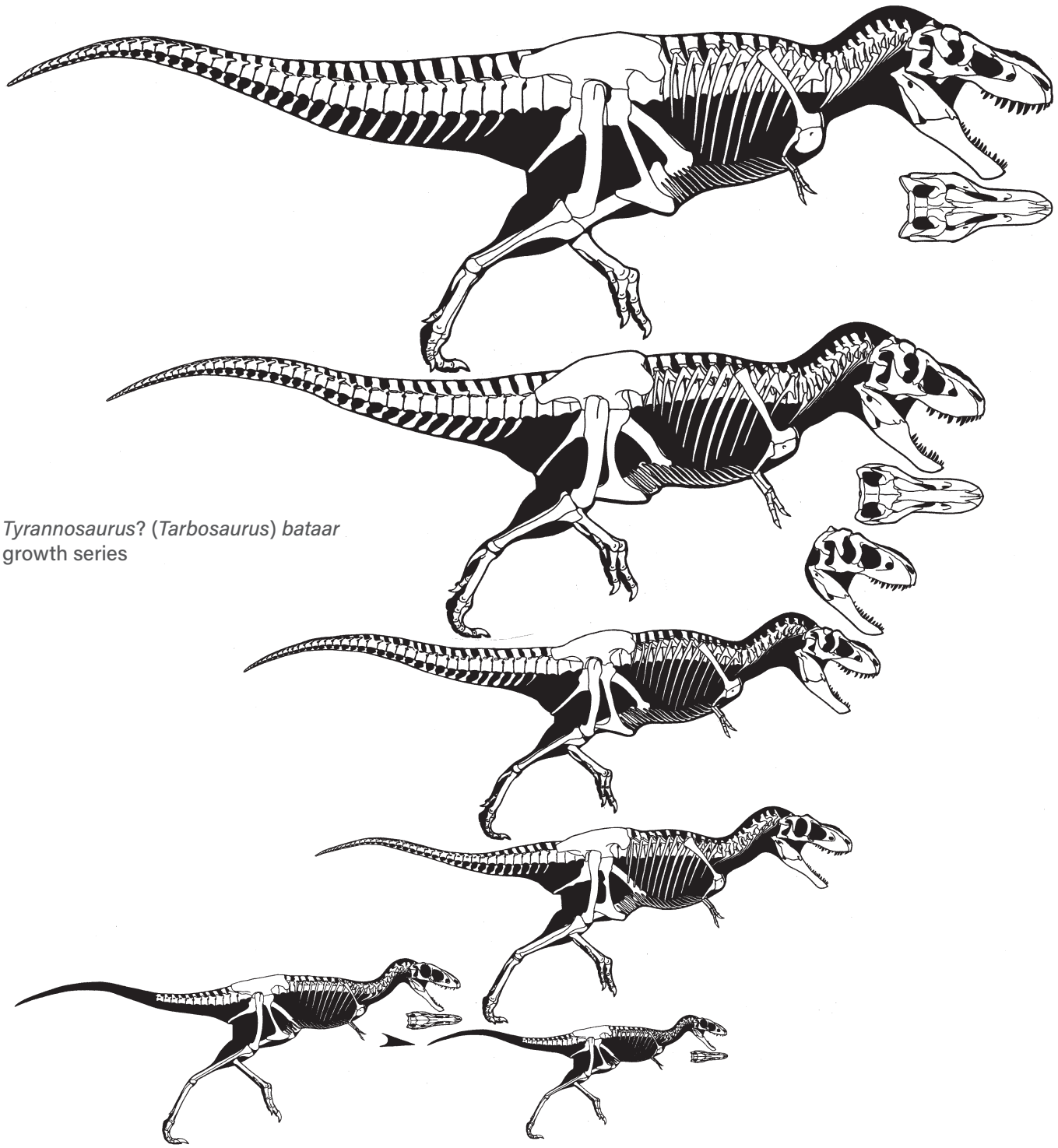
Nanuqsaurus (or *Tyrannosaurus*) *hoglundi*

— 8 m (27 ft) TL, 2.5 tonnes
FOSSIL REMAINS Small minority of skull, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern Alaska; middle Prince Creek.
HABITAT/S Well-watered coastal woodland, cool summers, severe winters including heavy snows.
NOTES Based on inadequate remains, is included because indicates presence of a tyrannosaurid in a harsh Arctic environment. Thought to be a dwarf tyrannosaur, other remains indicate was large. Possibly heavily feathered, especially in winter. May be a member of *Tyrannosaurus*, or ancestral to American members of genus, or unrelated.

Tyrannosaurus? (*Tarbosaurus*) *bataar*

— 9.5 m (31 ft) TL, 4 tonnes
FOSSIL REMAINS A number of skulls and skeletons from juvenile to adult, completely known. Small skin patches.
ANATOMICAL CHARACTERISTICS Head very large, but even largest examples are not broad aft, no erect brow hornlet, supraorbital boss knob shaped, not highly prominent, teeth not exceptionally large and robust, usually two small incisors at tip of dentary, otherwise as for *T. rex*. Skeleton moderately robust.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.

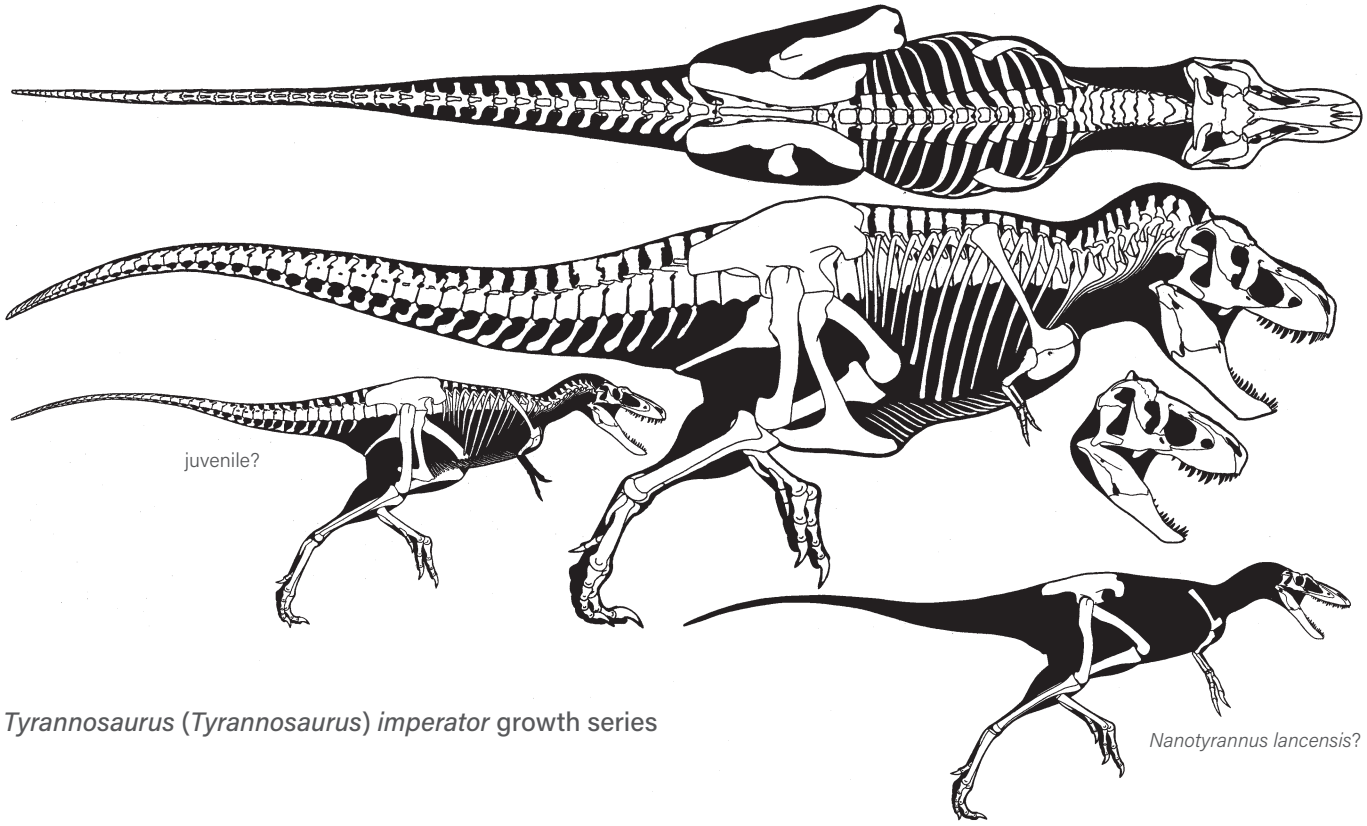
Tyrannosaurus (*Tarbosaurus*) *bataar*
(see also next page)



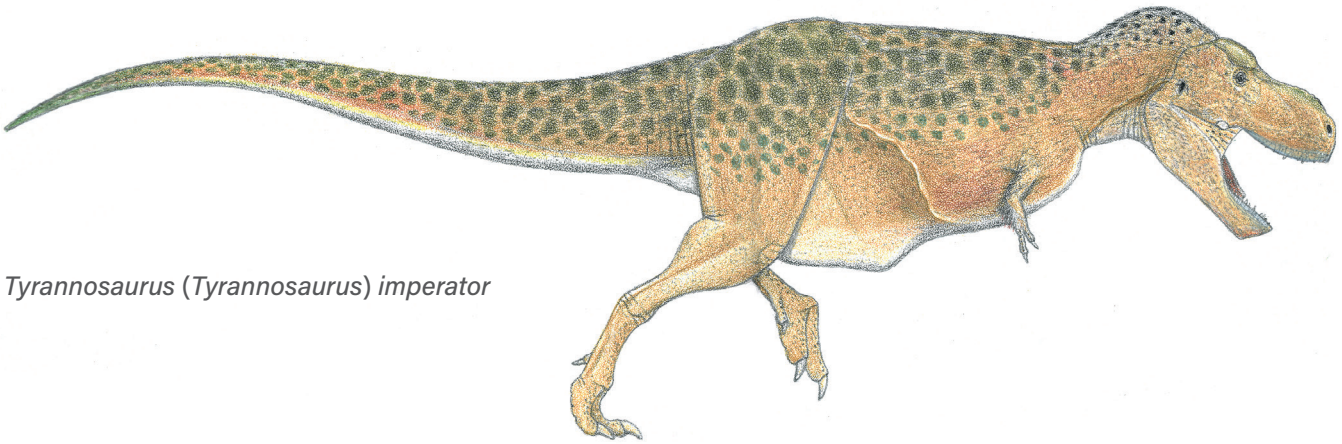
Tyrannosaurus? (*Tarbosaurus*) *bataar*
growth series

DISTRIBUTION AND FORMATION/S Mongolia and northern China; lower? Nemegt, Nemegt Svita, Yuanpu, Quipa, etc.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
HABITS Lacking large horned ceratopsids in its habitat, not as powerful as North American *Tyrannosaurus*.

NOTES Examples from levels other than original fossil may be different species; *Raptorex kriegstensis*, which is smallest skeleton in growth series, is probably a juvenile of this taxon. Very fragmentary *Zhuchengtyrannus magnus* indicates that a tyrannosaurine as large as *T. bataar* lived in the region a little earlier. May be close relative of American *Tyrannosaurus*.



Tyrannosaurus (*Tyrannosaurus*) *imperator* growth series



Tyrannosaurus (*Tyrannosaurus*) *imperator*

Tyrannosaurus (*Tyrannosaurus*) *imperator*

— 12 m (40 ft) TL, 7.5 tonnes

FOSSIL REMAINS A number of skulls and skeletons, other remains, completely known.

ANATOMICAL CHARACTERISTICS Overall build robust. Boss above orbit elongated spindle shape at least in large males, does not project strongly above top of head. Usually two small incisors at tip of dentary, otherwise as for *T. rex*.

AGE Late Cretaceous, late Maastrichtian.

DISTRIBUTION AND FORMATION/S Montana, Dakotas, Wyoming; lower Lance, Hell Creek.

HABITAT/S Well-watered coastal woodlands, climate cooler than in latest Maastrichtian, possibly chilly in winter.

HABITS Same as for *T. rex*.

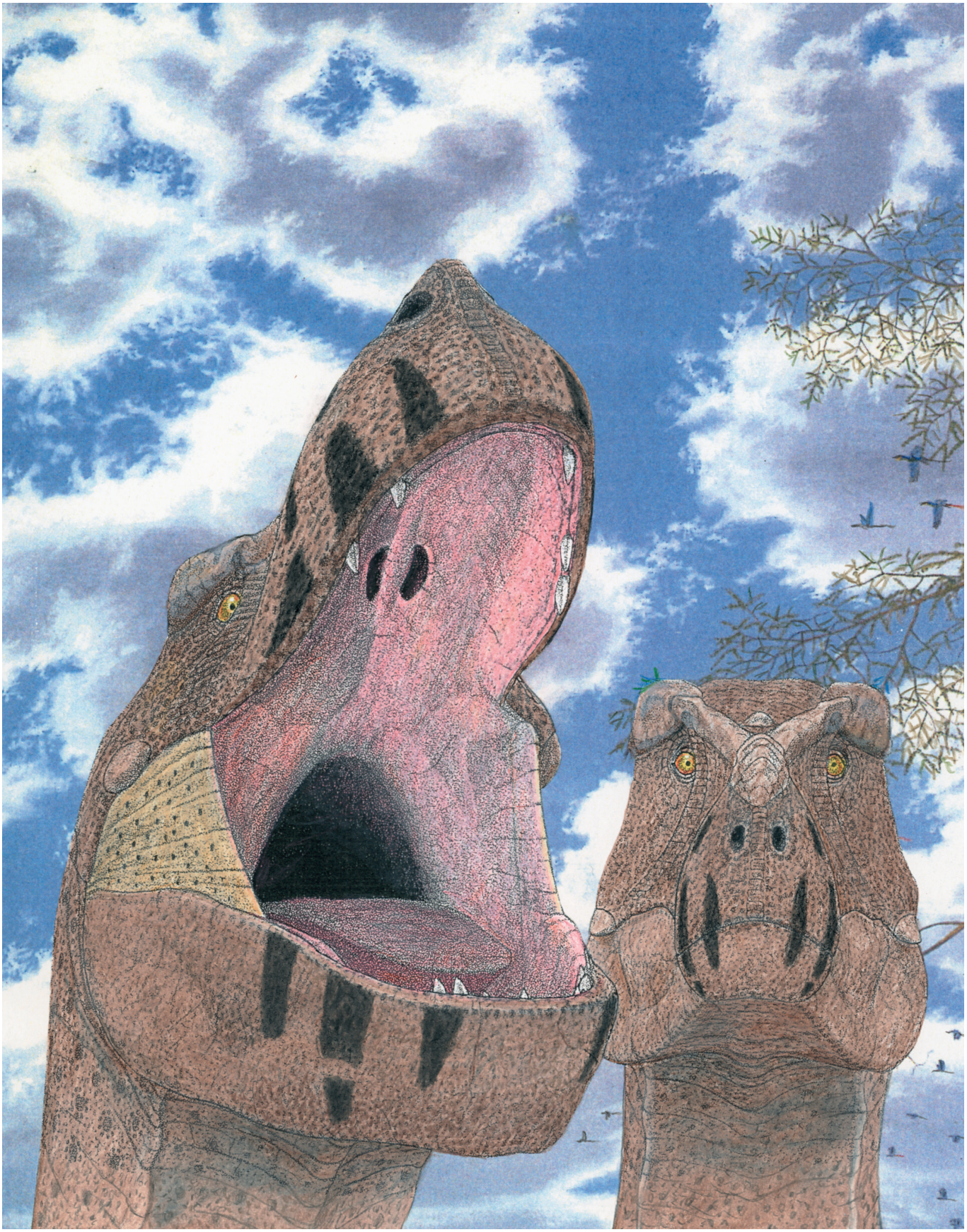
NOTES This species retained the ancestral tyrannosaurid condition of robust femora and two incisors, may be ancestral to either or both of the later *Tyrannosaurus* species. Absence from Canada is due to lack of formations north of border at that time, fragmentary fossils may be of species from more southerly US locations.

Tyrannosaurus (*Tyrannosaurus*) *rex*

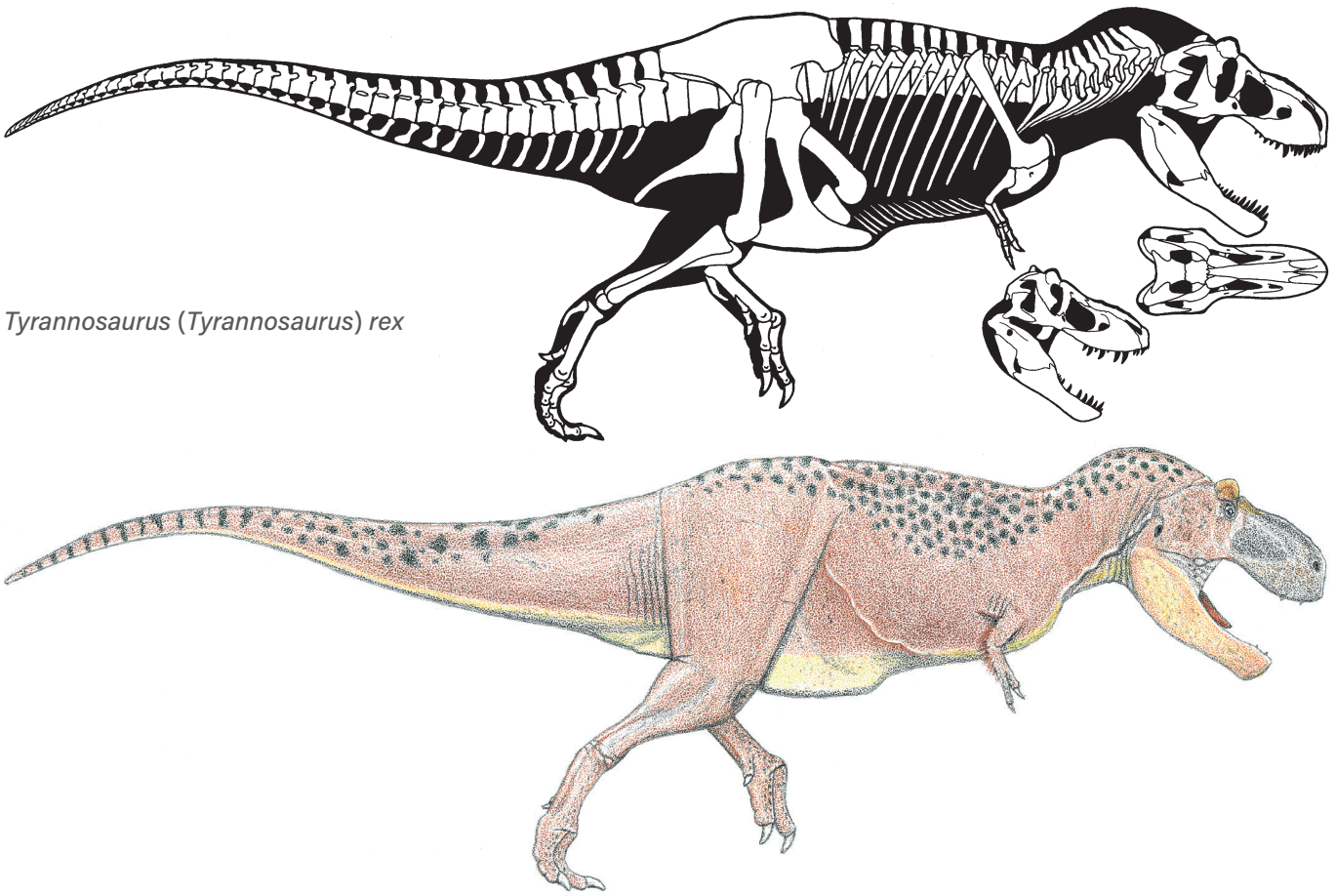
— 12 m (40 ft) TL, 7.5 tonnes

FOSSIL REMAINS A number of skulls and skeletons, other remains, completely known.

ANATOMICAL CHARACTERISTICS Overall build robust. Skull much more heavily constructed and stouter than those of other tyrannosaurids, back of skull especially



Tyrannosaurus imperator



Tyrannosaurus (*Tyrannosaurus*) *rex*

broad to accommodate oversized jaw and neck muscles; no other land predator with as powerful a bite; eyes face more strongly forward, increasing overlap of fields of vision; snout also broad. Lower jaws very deep. No erect brow hornlet at least in adults, boss above orbit is a knob-shaped disk that projects well above top of head at least in large males. One small incisor at tip of dentary, most teeth unusually large and conical. Neck very stout.
AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Montana, Dakotas, Wyoming, Colorado, Alberta, Saskatchewan; upper Lance and Hell Creek, Ferris, Denver, Frenchman, Scollard, Willow Creek.
HABITAT/S Well-watered coastal woodlands, climate warmer than earlier in Maastrichtian.
HABITS An extreme version of the tyrannosaurid form; healed wounds on adult hadrosaurs and ceratopsids indicate that adults hunted similarly elephant-sized prey on a regular basis, using the tremendously powerful head and teeth to lethally wound victims. Such firepower and size were more than needed to hunt less-dangerous juveniles or just adult hadrosaurs, which made up a minority of the herbivore population dominated by dangerous horned *Triceratops prorsus*.
NOTES *Tyrannosaurus* skeletons were once very rare, high financial value encouraged the discovery of dozens of fossils, all of which were placed in *T. rex*. Unusually great variation in the robustness of the fossils, shifts in the number of dentary incisors, strong differences in the shapes of the supraorbital bosses used to distinguish species, and the differential pattern of distribution of varying robustness not being uniform throughout the stratigraphic range, as should be true if the robusts and graciles were females and males, indicate that multiple species evolved over some 1.5 million years. If correct, then the main competitor of robust *T. rex* was the more gracile *T. regina*, with *T. rex* possibly more specialized in preying on massive *Triceratops*. Assignment of fossils from locations well to the south of Montana and South Dakota to *T. rex* or *Tyrannosaurus* is highly problematic. The great width of the aft skull probably evolved to maximize power of the jaw muscles, and the forward-facing eyes with overlapping fields of vision may have been a secondary result.

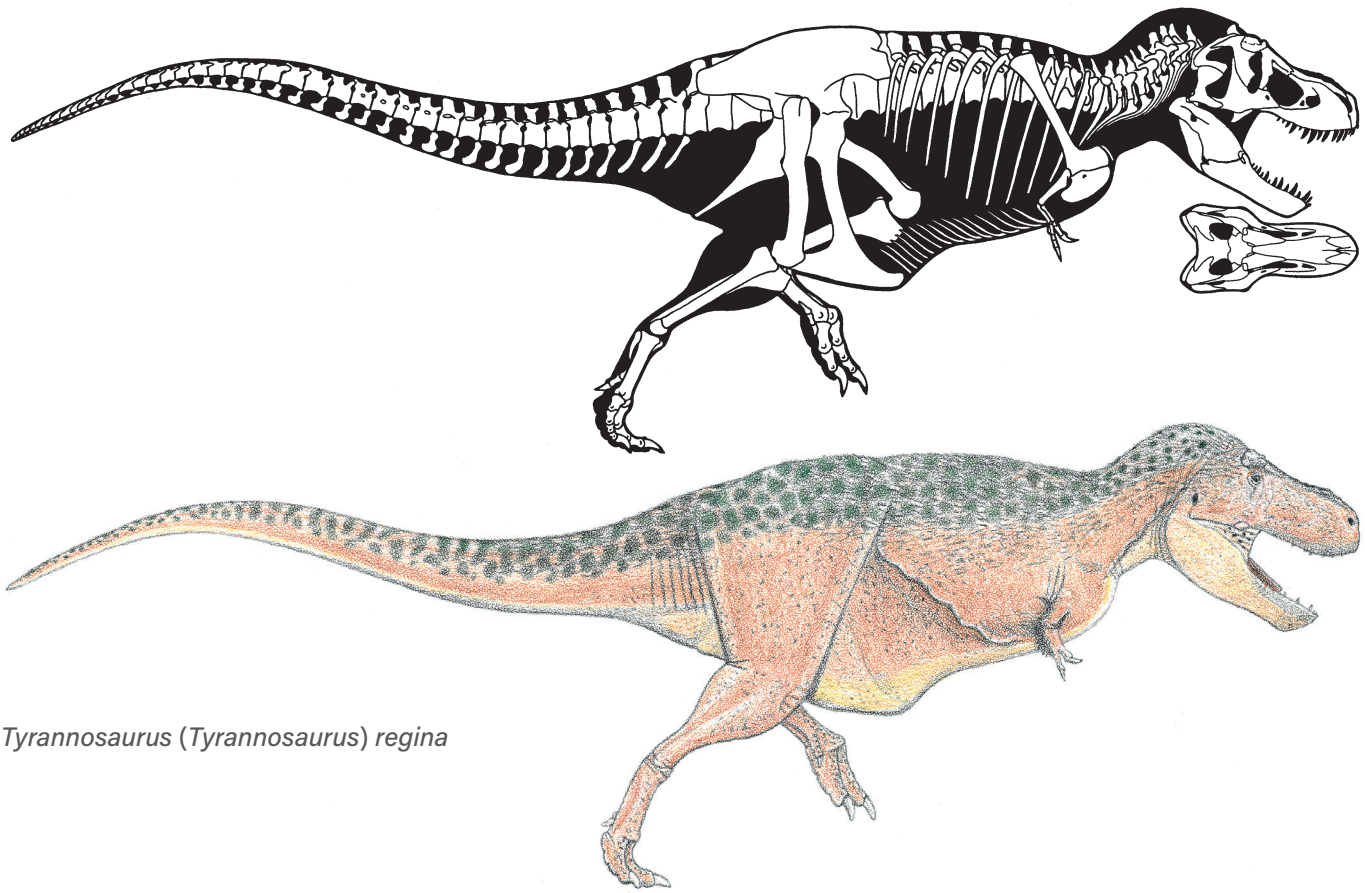
Tyrannosaurus (*Tyrannosaurus*) *regina*

— 12 m (40 ft) TL, 7.5 tonnes
FOSSIL REMAINS A number of skulls and skeletons, other remains, completely known.
ANATOMICAL CHARACTERISTICS Overall build of skull and skeleton more gracile. Boss above orbit does not project strongly above head. One small incisor at tip of dentary, otherwise similar to *T. rex*.

AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Montana, Dakotas, Wyoming, Colorado, Alberta, Saskatchewan; upper Lance and Hell Creek, Ferris, Denver, Frenchman, Scollard, Willow Creek.
HABITAT/S Well-watered coastal woodlands, climate warmer than earlier in Maastrichtian.
HABITS Same as for *T. rex*, except perhaps better adapted for hunting less common edmontosaurs.
NOTES Two species of *Tyrannosaurus* probably present in same region at the final extinction. Fragmentary *T. megagracilis* may be juvenile of this or of *T. rex*.

?*Nanotyrannus lancensis*

— Adult size uncertain
FOSSIL REMAINS At least one skull, juvenile or subadult.
ANATOMICAL CHARACTERISTICS Medium sized, very gracile. Small lacrimal hornlet present; back of skull especially broad; eyes face more strongly forward, increasing overlap of fields of vision, teeth modest-sized blades. Lower arm and especially hand very elongated, hand longer than that of adult *Tyrannosaurus*.
DISTRIBUTION AND FORMATION/S Montana; lower? Hell Creek.
HABITAT/S Well-watered coastal woodlands, climate warmer than earlier in Maastrichtian.
HABITS Assuming the known fossils are near adult size, pursued similar-sized dinosaurs including ornithomimids.
NOTES A modest number of very gracile tyrannosaurid remains from the same formations as *Tyrannosaurus* have been considered its juveniles, distinct species, or one or the other. That the original fossil of *N. lancensis* is only a distorted skull hinders assessing the possibilities. A complete fossil, also from the lower Hell Creek, that may be the same species has a very large lower arm and hand that precludes it being a juvenile of contemporary *T.imperator*. Another, largely complete fossil from the lower Hell Creek may be a juvenile *T. imperator*, but absence of its lower arm precludes full assessment. If such are juveniles of massive *Tyrannosaurus*, then no other avepod is known to have undergone such an extreme change in form with growth, including a shift from bladed to massive conical teeth; if real, the drastic transformation with growth is probably a result of the radical shift from hunting fast prey such as ornithomimids to elephant-sized, fast-charging adult horned dinosaurs. If the nanotyrannos are instead distinct taxa, then the situation was similar to that in Asia, where gracile alioraminians and stout tarbosaurs shared the same habitats.



Tyrannosaurus (*Tyrannosaurus*) *regina*

— NEOCOELUROSAURS

SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS COELUROSAURS OF THE LATE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Heads from large to small, brow hornlet absent, toothed to toothless and beaked, when teeth present serrations tend to be reduced in some manner or absent. Necks moderately to very long. Tails very long to very short. Shoulder girdles usually like those in birds, with horizontal scapula blades and vertical, anterior-facing coracoids, arms very long to short, large, semilunate inner carpal block that further increased wrist flexion usually present, hands usually long, fingers from three to one. Brains enlarged, semiavian in form.
ONTOGENY Growth rates apparently moderate.
HABITS Reproduction generally similar to that of ratites and tinamous; in at least some cases males incubated the eggs and were probably polygamous; egg hatching in a given clutch not synchronous.
NOTES Neocoelurosaurs are more derived than tyrannosauroids; some examples such as *Bicentenaria*, *Sciurumimus*, and *Zuolong* may be basal to this group.

— NEOCOELUROSAUR MISCELLANEA

SMALL NEOCOELUROSAURS OF THE LATE JURASSIC TO THE LATE CRETACEOUS.

ANATOMICAL CHARACTERISTICS Uniform. Heads small to moderately large, elongated, crests absent. Skeletons gracile. Tails long. Arms and hands well developed. Legs and feet long and slender.
HABITS Fast small game hunters, also fishers, similar in function to earlier coelophysids.
NOTES The classic small coelurosaurs were a widespread element in dinosaur faunas, the generalized small canids of their time; relationships often uncertain and group splittable into subdivisions.

Bicentenaria argentina

— 3 m (10 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Partial skull and skeletal elements.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; upper Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

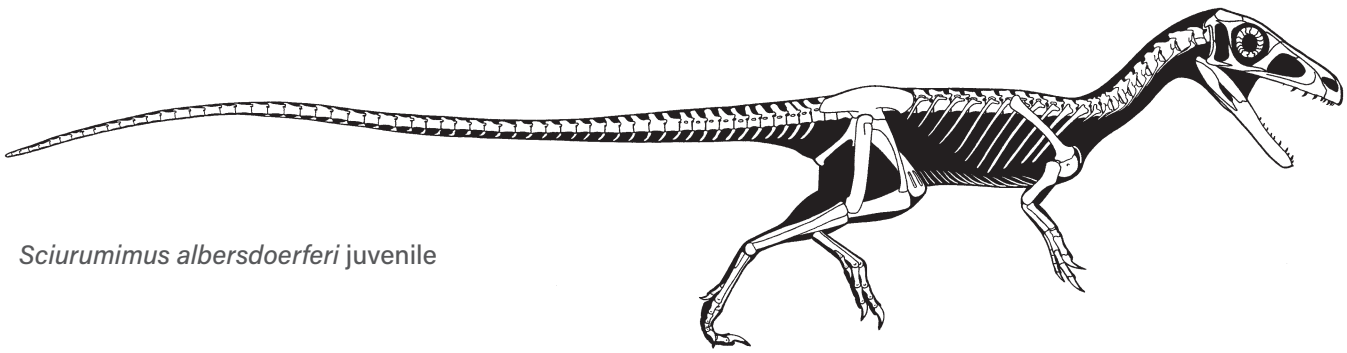
Sciurumimus albersdoerferi

— Adult size uncertain
FOSSIL REMAINS Complete juvenile skull and skeleton, extensive external fibers.
ANATOMICAL CHARACTERISTICS Insufficient information due to juvenile status of fossil.
AGE Late Jurassic, late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Southern Germany; upper Rögling.

Zuolong salleei

— 3 m (10 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, early Oxfordian.

Zuolong salleei



Sciurumimus albersdoerferi juvenile

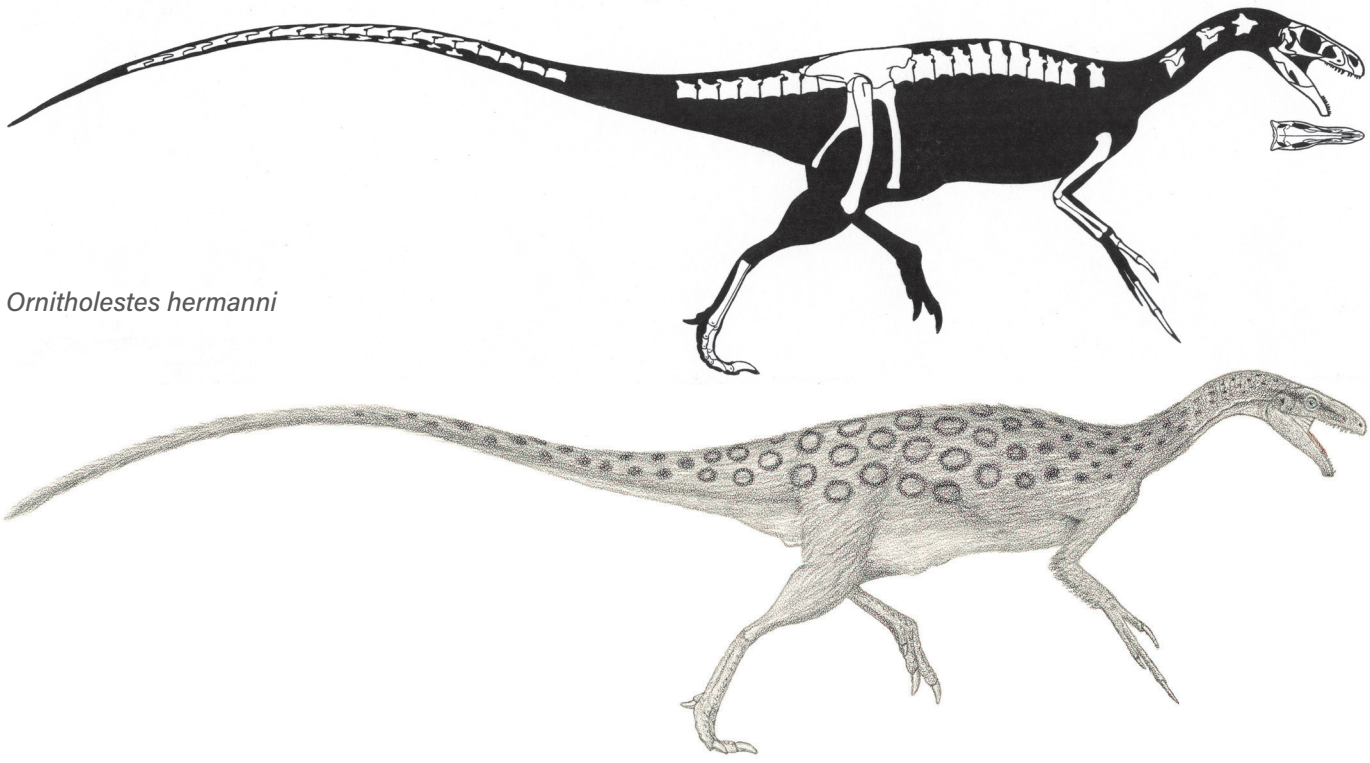
DISTRIBUTION AND FORMATION/S
Northwestern China; upper Shishugou.
HABITAT/S Well-watered woodlands with short dry season.

Ornitholestes hermanni
— 2 m (7 ft) TL, 14 kg (30 lb)
FOSSIL REMAINS Nearly complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular, rather small relative to body, teeth on lower jaw restricted to front end. Leg moderately long.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Hunted small game as well as fished.
NOTES A classic coelurosaur.

Coelurus fragilis
— 2.5 m (8 ft) TL, 25 kg (50 lb)
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Lightly built. Fingers long and slender.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Able to pursue faster prey than *Ornitholestes*.
NOTES Remains imply close relatives higher in the Morrison. This and *Tanycolagreus* may form the family Coeluridae.

Tanycolagreus topwilsoni
— 4 m (13 ft) TL, 120 kg (250 lb)
FOSSIL REMAINS Much of the skull and majority of the skeleton.
ANATOMICAL CHARACTERISTICS Head large, long, subrectangular. Leg long and gracile.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Prey included fairly large game.

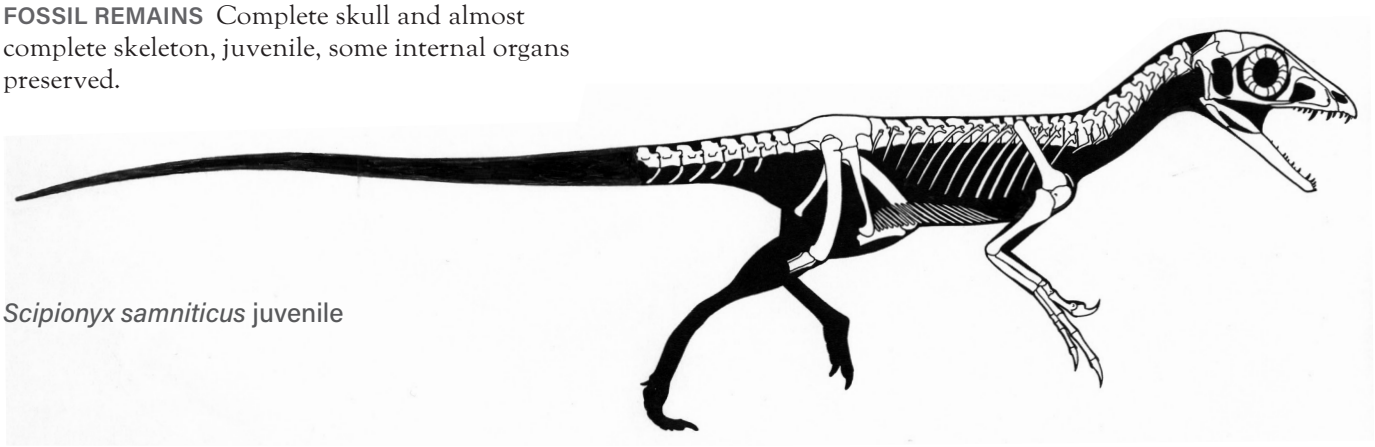
Nedcolbertia justinhofmanni
— Adult size uncertain
FOSSIL REMAINS Minority of several skeletons, immature.
ANATOMICAL CHARACTERISTICS Leg long and gracile.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.



Ornitholestes hermanni

Aniksosaurus darwini
— 2.5 m (9 ft) TL, 30 kg (65 lb)
FOSSIL REMAINS Several partial skeletons.
ANATOMICAL CHARACTERISTICS Robustly built. Posterior pelvis broad.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.
ANATOMICAL CHARACTERISTICS Proportions characteristic for juvenile.
AGE Early Cretaceous, early Albian.
DISTRIBUTION AND FORMATION/S Central Italy; unnamed formation.
HABITS Juveniles hunted small vertebrates, insects.
NOTES May be the juvenile of much larger abelisaur or carcharodontosaur, or of a compsognathid. Intestinal tract has a preavian condition.

Scipionyx samniticus
— Adult size uncertain
FOSSIL REMAINS Complete skull and almost complete skeleton, juvenile, some internal organs preserved.



Scipionyx samniticus juvenile

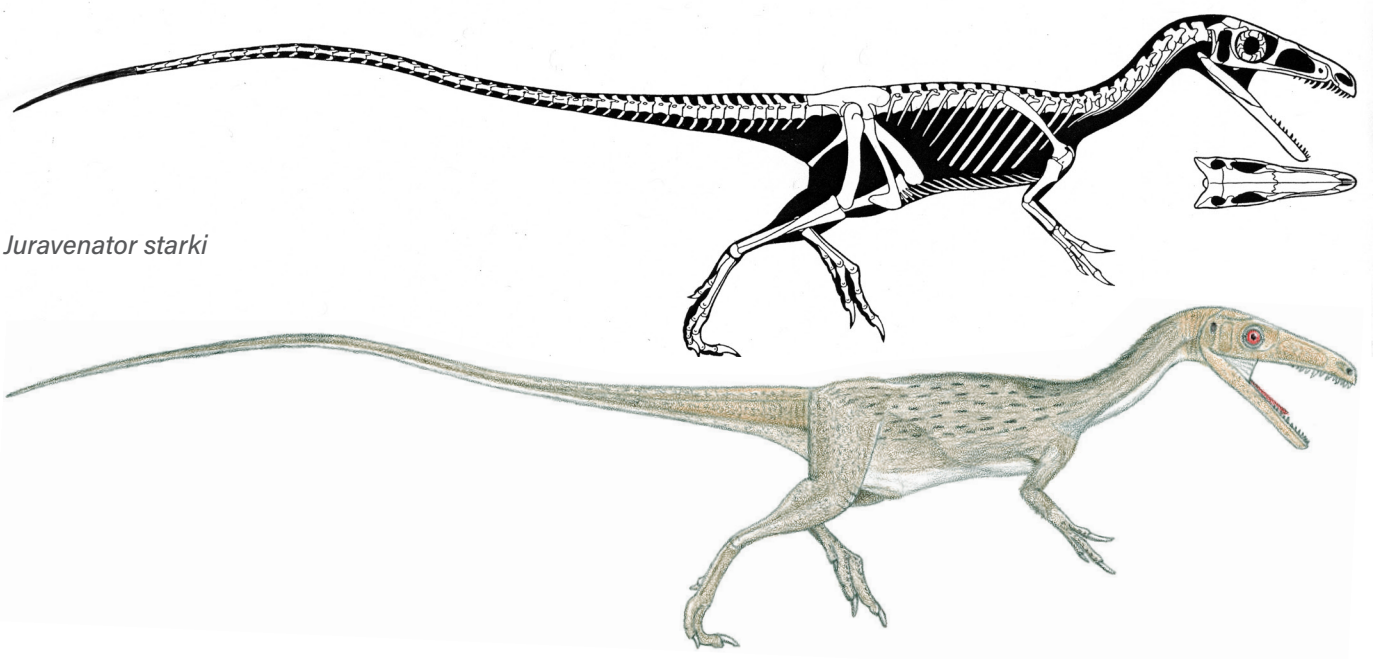
— COMPSOGNATHIDS

SMALL PREDATORY NEOCOELUROSAURS LIMITED TO THE LATE JURASSIC AND EARLY CRETACEOUS OF EURASIA AND SOUTH AMERICA.

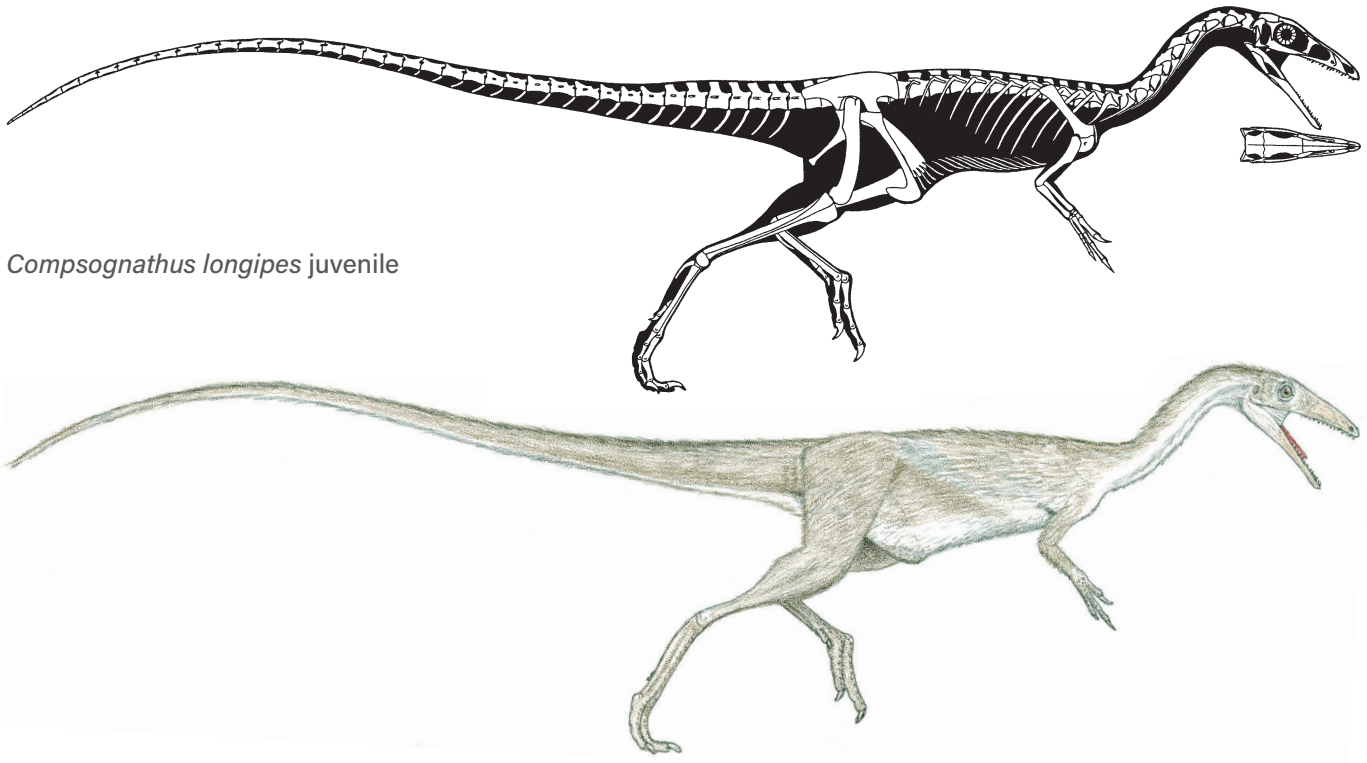
ANATOMICAL CHARACTERISTICS Uniform. In most regards standard for small neocoelurosaurs. Necks moderately long. Tails quite long. Hands strongly asymmetrical because thumbs and claws unusually stout and outer fingers slender. Boots on pubes large; legs moderately long.
HABITS Ambushed and chased small game, also fish in some cases. Thumb an important weapon for hunting and/or combat within species.
NOTES A common and widely distributed group of small neocoelurosaurs, the foxes of their time.

Juravenator starki (see p.136)
— Adult size uncertain
FOSSIL REMAINS Nearly complete juvenile skull and skeleton, small skin patches, external fibers.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout fairly deep, indentation in snout, teeth large. Scapula blade slender. Skin with small scales on leg and tail, some of body covered by fibers, full extent of either uncertain.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Southern Germany; lower Painten.
HABITAT/S Found as drift in lagoonal deposits near probably arid, brush-covered islands.
HABITS Large teeth indicate it hunted fairly large animals; kink in upper jaw indicates it also fished.
NOTES Indicates that some dinosaurs bore both bare body skin and feathers, like some birds.

Compsognathus longipes (see p.136)
— Adult size uncertain
FOSSIL REMAINS Nearly complete skull and skeleton, possibly juvenile.
ANATOMICAL CHARACTERISTICS Head shallow, subtriangular, teeth small.
AGE Late Jurassic, middle or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Southern Germany; Painten, level uncertain.
HABITAT/S Found as drift in lagoonal deposits near probably arid, brush-covered islands.
NOTES The second dinosaur known from a largely complete skull and skeleton. Large head relative to larger-bodied *C. corallestris* suggests is a juvenile, but head is not large compared to those of other adult compsognathids.



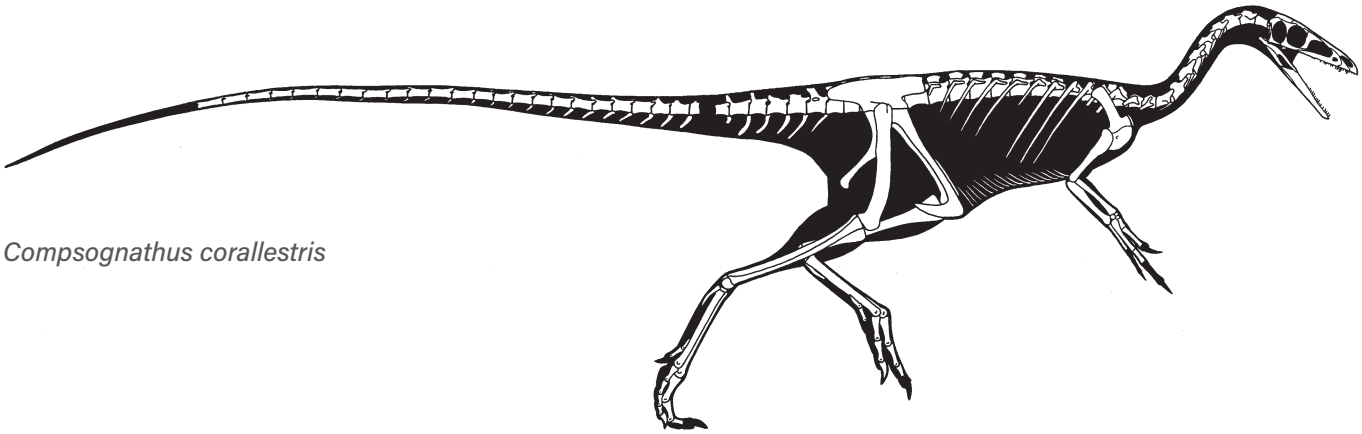
Juravenator starki



Compsognathus longipes juvenile

Compsognathus corallestris

— 1.2 m (4 ft) TL, 2.1 kg (4.5 lb)
FOSSIL REMAINS Skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head small, shallow, subtriangular, teeth small.
AGE Late Jurassic, early Tithonian.
DISTRIBUTION AND FORMATION/S Southern France; unnamed formation.
HABITAT/S Found as drift in lagoonal deposits near probably arid, brush-covered islands.
NOTES Usual placement in earlier *C. longipes* from different island problematic.



Compsognathus corallestris

"Ubirajara jubatus"

— Adult size uncertain

FOSSIL REMAINS Partial skeleton, possibly juvenile, extensive external fibers.

ANATOMICAL CHARACTERISTICS Mane of long bristle fibers over neck and back, pair of elongated ribbon feathers on side of each shoulder.

AGE Early Cretaceous, Aptian.

DISTRIBUTION AND FORMATION/S Northeastern Brazil; Crato.

HABITS Used long shoulder feathers for display, may have begun to reproduce before fully grown.

NOTES Dispute over national ownership of fossil has led to name being potentially officially withdrawn.

Sinosauropteryx prima

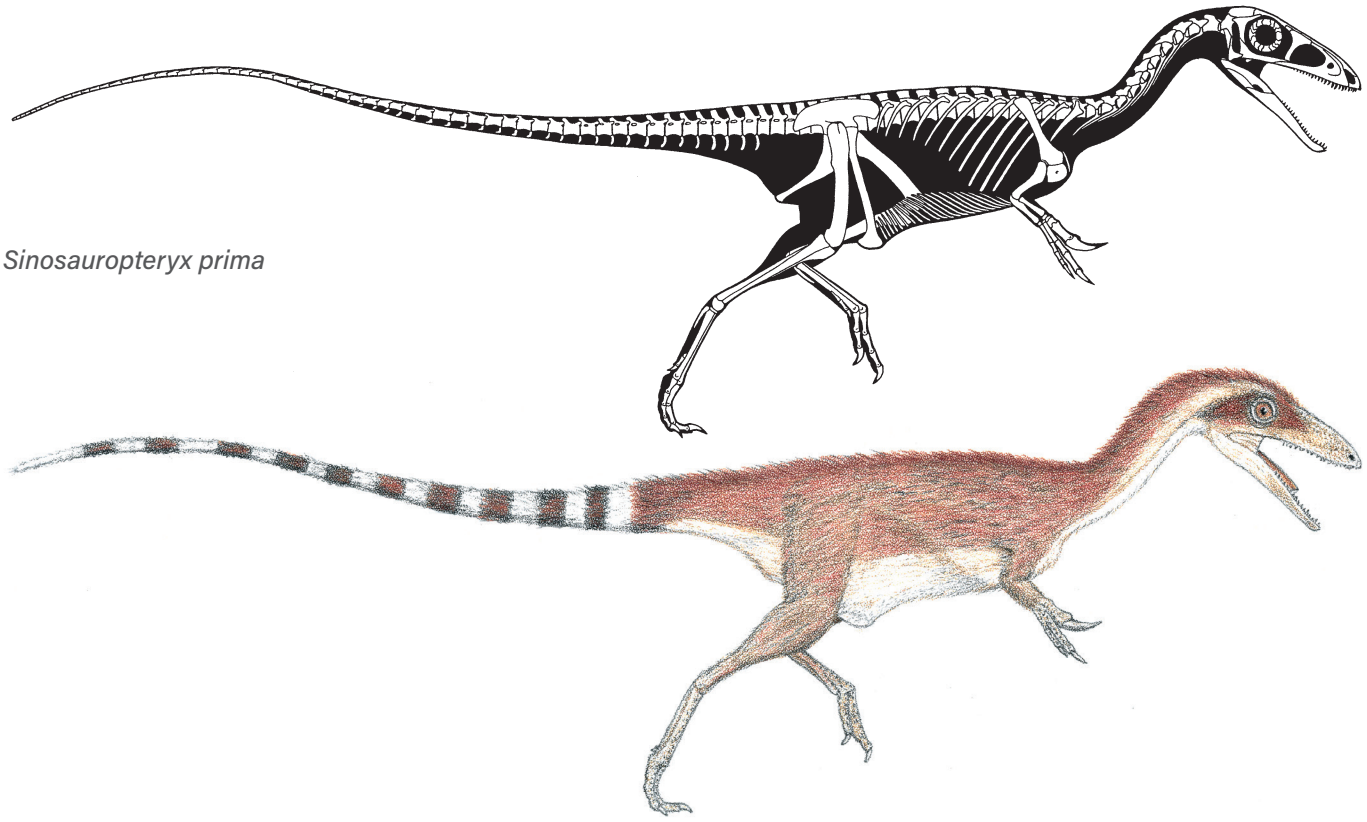
— 1 m (3 ft) TL, 1.2 kg (2.5 lb)

FOSSIL REMAINS A few complete skulls and skeletons, extensive external fibers, internal organs.

ANATOMICAL CHARACTERISTICS Snout subtriangular, teeth small. Arm shorter and thumb and claw stouter than in other compsognathids. Simple protofeathers on most of head except front of snout and most of body except hands and feet; protofeathers atop head and body, possible bandit mask, and dark bands on tail dark brown or reddish brown. Elongated eggs 4 cm (1.5 in) long.

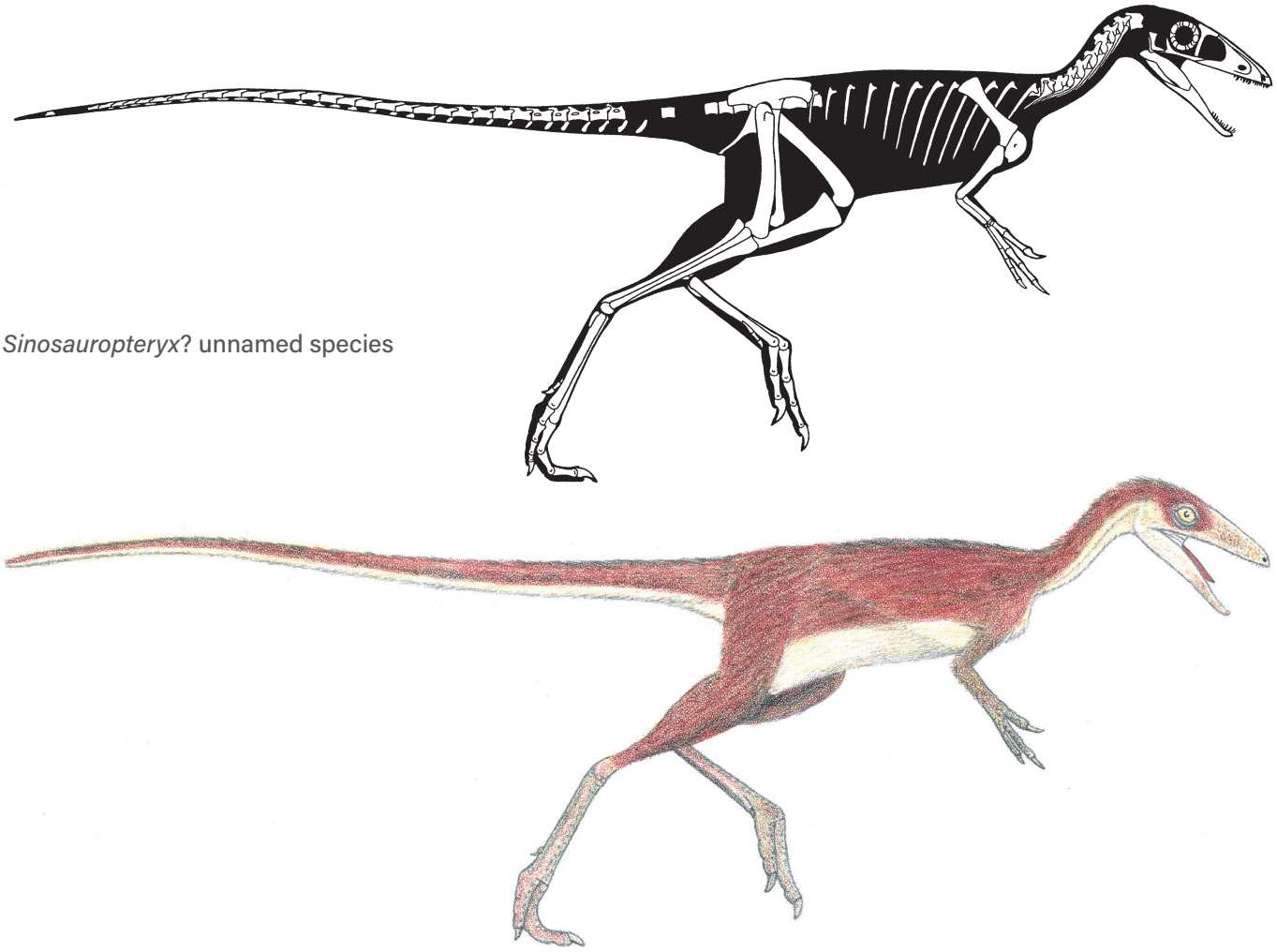
AGE Early Cretaceous, latest Barremian and earliest Aptian.

DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.



Sinosauropteryx prima

Sinosauropteryx prima and *Confuciusornis sanctus*



Sinosauropteryx? unnamed species

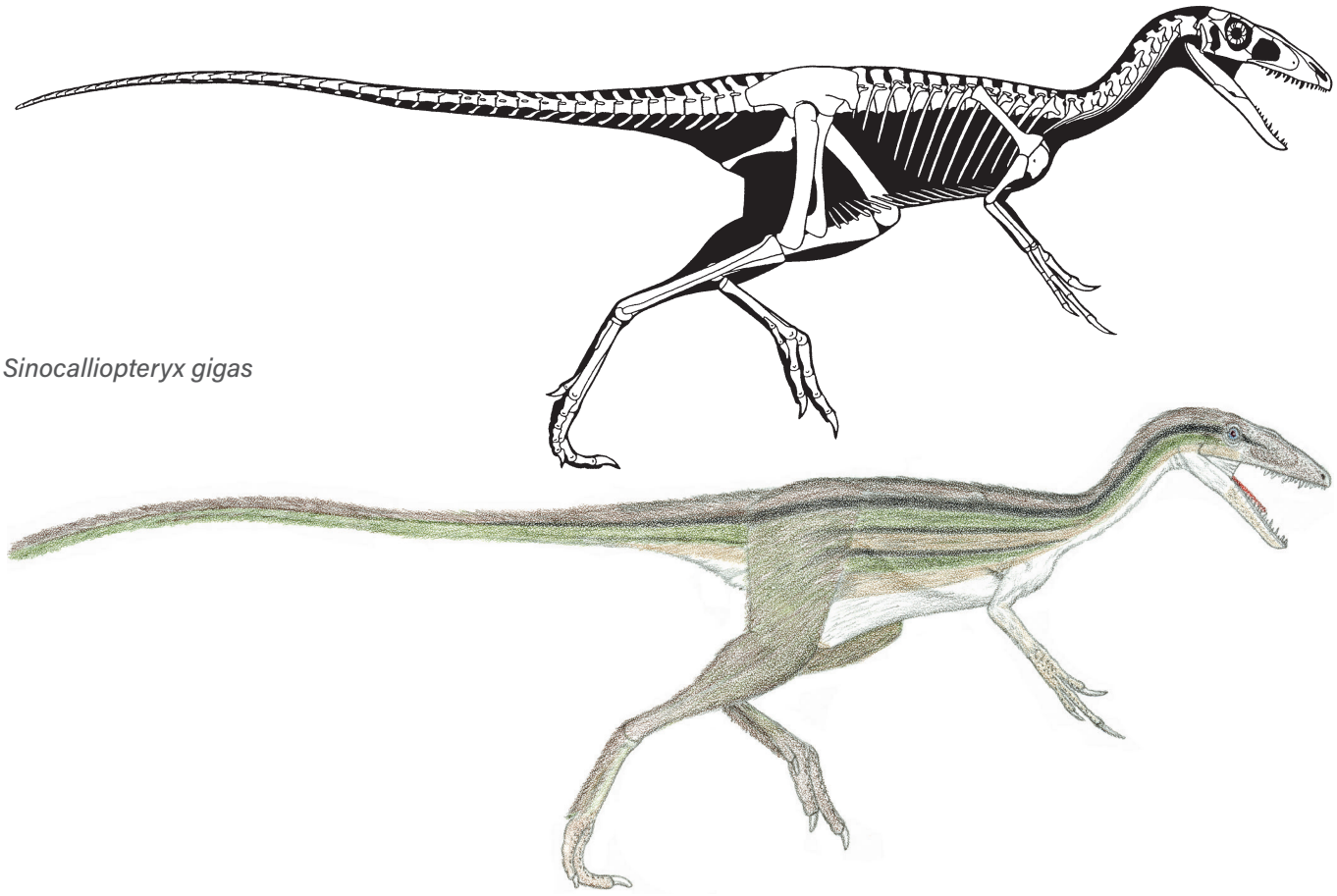
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Internal remains once interpreted as eggs are instead intestines. The dinosaur whose life appearance is best understood including coloration, and the one whose appearance may have been restored close to correctly.

Sinosauropteryx? unnamed species?

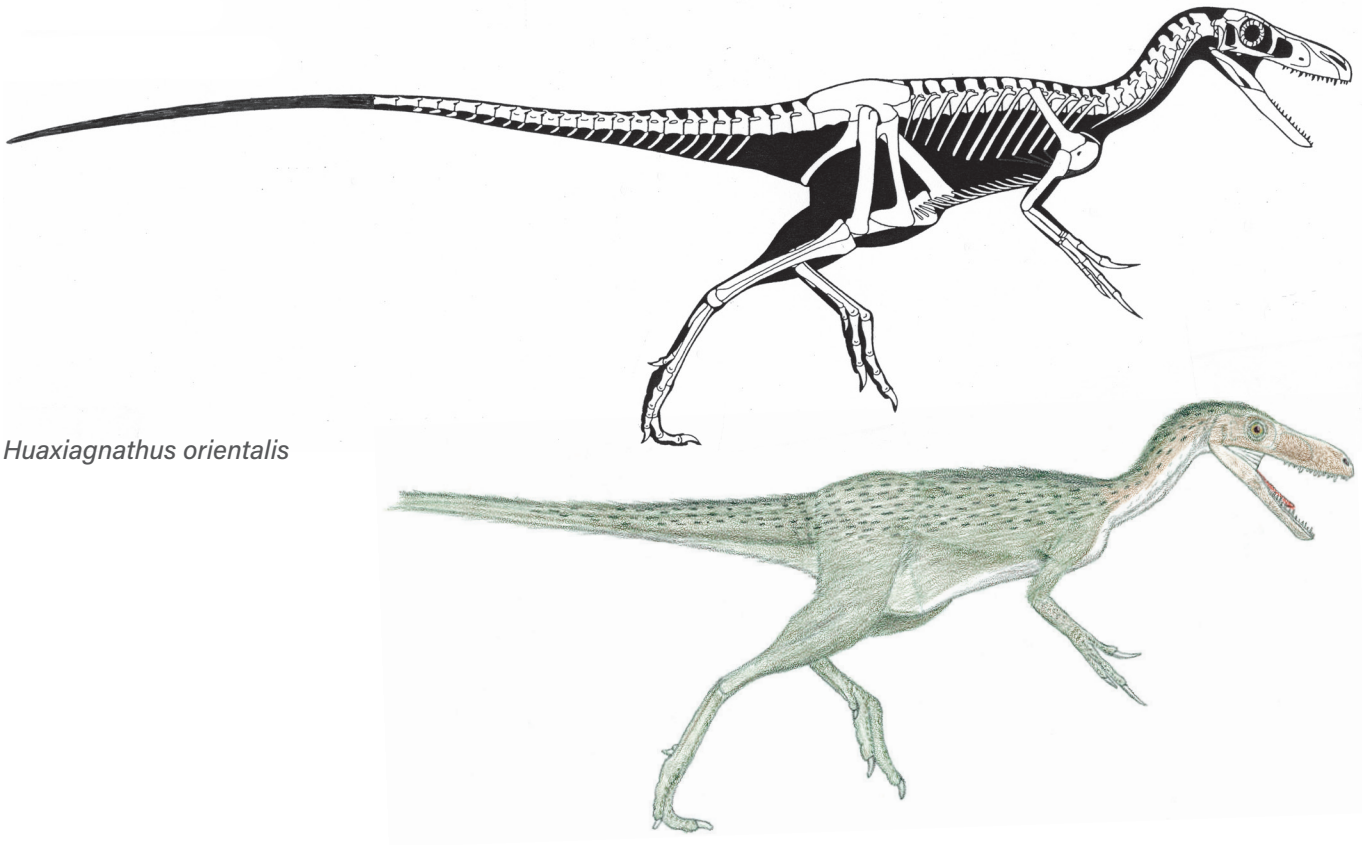
— 1 m (3 ft) TL, 1.3 kg (2.8 lb)
FOSSIL REMAINS Nearly complete skull and skeleton, some external fibers.
ANATOMICAL CHARACTERISTICS Head subtriangular, teeth large. Tail rather short. Arm and hand rather small. Leg long. Simple protofeathers over most of body including tuft at end of tail, protofeathers atop head, body, and tail dark brown or reddish brown. Tail not banded.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Usual placement in *S. prima* problematic unless is a smaller-armed gender morph.

Sinocalliopteryx gigas (see p.140)

— 2.3 m (7.5 ft) TL, 21 kg (45 lb)
FOSSIL REMAINS Complete skull and skeleton, extensive external fibers.
ANATOMICAL CHARACTERISTICS Head subtriangular, small paired crestlets atop snout, teeth fairly large. Tail rather short. Leg long. Simple protofeathers over most of body including upper feet, especially long at hips, tail base, and thigh, forming tuft at end of tail.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Hunted larger prey than smaller *Huaxiagnathus.* Foot feathers probably for display.



Sinocalliopteryx gigas



Huaxiagnathus orientalis

Huaxiagnathus orientalis
— 1.7 m (5.5 ft) TL, 6 kg (13 lb)
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular, front fairly deep, teeth not very large.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Hunted larger prey than smaller *Sinosauropteryx*.

Aristosuchus pusillus
— 2 m (6 ft) TL, 8 kg (18 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Barremian.
DISTRIBUTION AND FORMATION/S Southern England; Wessex.

Mirischia asymmetrica
— 2 m (6 ft) TL, 8 kg (18 lb)
FOSSIL REMAINS Minority of skeleton. Some internal organs preserved.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Cretaceous, probably Albian.
DISTRIBUTION AND FORMATION/S Eastern Brazil; Santana.
NOTES Found as drift in nearshore marine sediments.

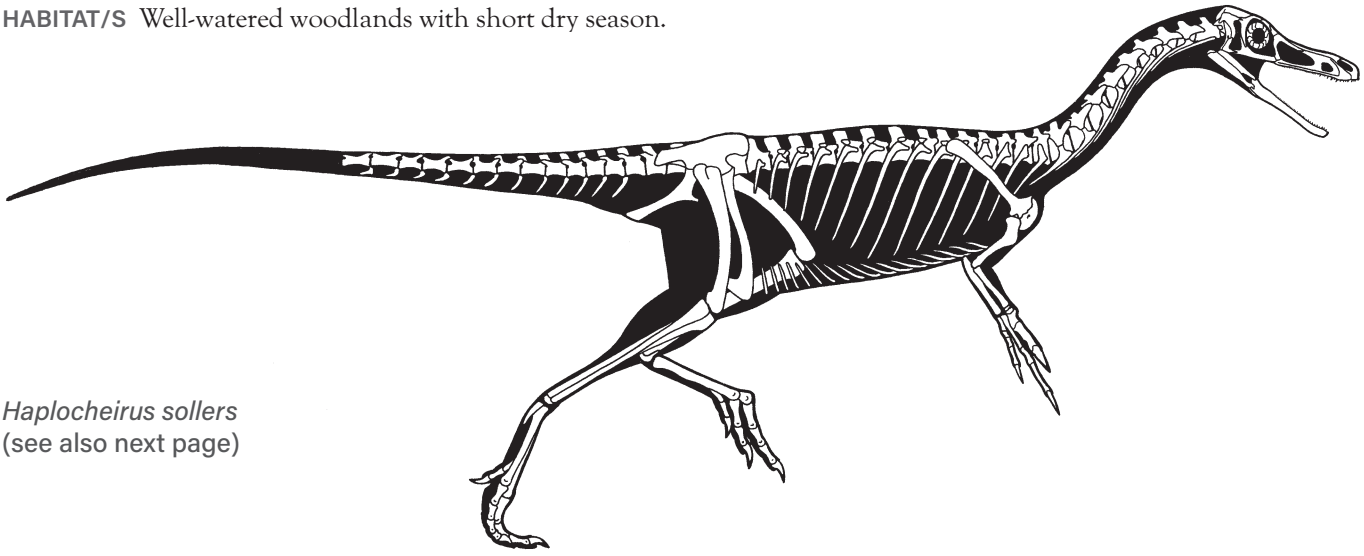
— HAPLOCHEIRIDS
SMALL NEOCOELUROSAURS LIMITED TO THE LATE JURASSIC OF ASIA.

ANATOMICAL CHARACTERISTICS Teeth small, bladed, serrated, limited in number and to front third or half of jaws. Scapula blades slender, arms and hands moderately long. Feet moderately elongated.
NOTES Have been considered basal alvarezsaurs in part because of stout thumb of *Haplocheirus*, but at least as likely to be more closely related to ornithomimosaurs. Limited distribution may reflect lack of sufficient sampling.

Aorun zhaoi
Adult size uncertain
FOSSIL REMAINS Majority of juvenile skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Thumb not enlarged.
AGE Late Jurassic, late Callovian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Shishugou.
HABITAT/S Well-watered woodlands with short dry season.

Aorun zhaoi

Haplocheirus sollers
— 2 m (6 ft) TL, 21 kg (45 lb)
ANATOMICAL CHARACTERISTICS Thumb enlarged, other two fingers quite slender.
FOSSIL REMAINS Nearly complete skull and skeleton.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.
NOTES If not an alvarezsaur, enlarged thumb was an independent development.


Haplocheirus sollers
(see also next page)

Haplocheirus sollers

— ORNITHOMIMOSAURS

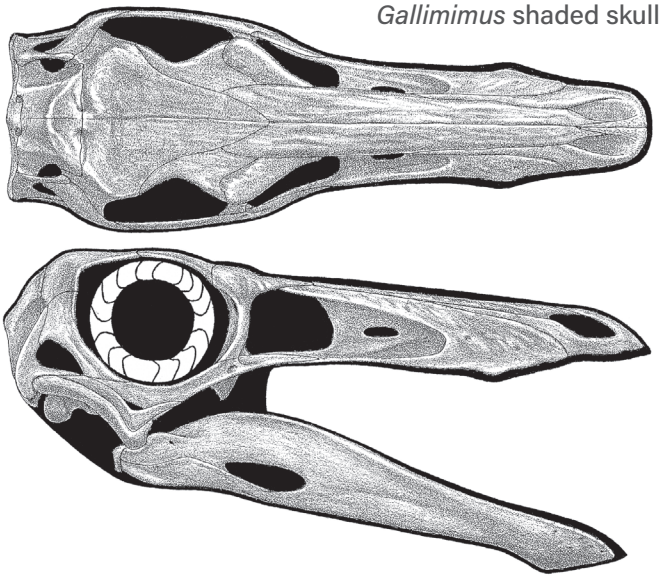
SMALL TO GIGANTIC NONPREDATORY NEOCOELUROSAURS OF THE CRETACEOUS OF NORTHERN HEMISPHERE AND AFRICA.

ANATOMICAL CHARACTERISTICS Usually uniform. Usually not heavily built. Heads small, shallow, and narrow, teeth reduced or absent and shallow, blunt beak present, eyes face partly forward, and some degree of stereo vision possible, extra joint in lower jaw absent. Necks long, at least fairly slender, ribs so short they do not overlap, increasing flexibility of neck. Scapula blades slender, semilunate carpal blocks absent and wrists not highly flexible, arms and hands long and slender. Legs long, toes short, claws not sharp. Brains semiavian in structure and size, olfactory bulbs reduced. Gizzard stones sometimes present.
HABITAT/S Well-watered areas.
HABITS Small, slender skulls, unhooked beaks, and lightly constructed necks bar these from being predators. Possibly omnivorous, combining some small animals and insects with plant material gathered with assistance of long arms and hands. Main defense speed, also kicks from powerful legs and slashing with large hand claws.
NOTES The dinosaurs most similar to ostriches and other big ratites. Fragmentary remains imply possible presence in Australia. Fragmentary Siberian *Lepidocheirosaurus natatilis* may indicate presence of group in Late Jurassic. A frequent and sometimes common element of Cretaceous faunas.

— BASO-ORNITHOMIMOSAURS

SMALL TO LARGE ORNITHOMIMOSAURS OF THE CRETACEOUS OF EURASIA.

ANATOMICAL CHARACTERISTICS Not as gracile as ornithomimids, pelves usually not as large, feet not as compressed, hallux usually still present. May be splittable into a larger number of subdivisions.
NOTES Baso-ornithomimosaurs are basal ornithomimosaurs excluding ornithomimids.

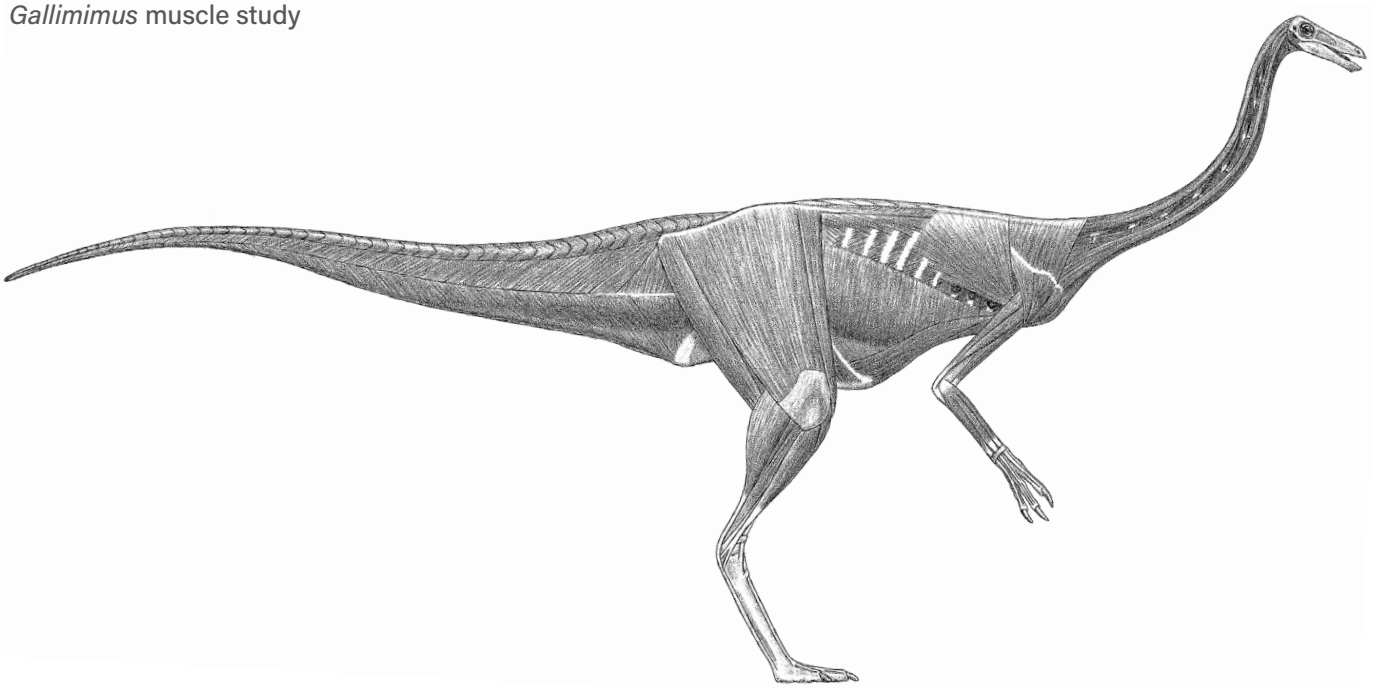


Gallimimus shaded skull

Nqwebasaurus thwazi

— 1 m (3 ft) TL, 1 kg (2.5 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Hand moderately long, thumb enlarged. Boot on pubis small, leg very long and gracile.

Gallimimus muscle study



AGE Late Jurassic or Early Cretaceous.
DISTRIBUTION AND FORMATION/S Southern South Africa; upper Kirkwood.
NOTES Indicates that at least early ornithomimosaurs were present in Southern Hemisphere, perhaps in the Late Jurassic.

Pelecanimimus polyodon

— 2.5 m (8 ft) TL, 30 kg (60 lb)
FOSSIL REMAINS Complete skull and front part of skeleton, some soft tissues.
ANATOMICAL CHARACTERISTICS Snout long and tapering, small hornlets above orbits, hundreds of tiny teeth concentrated in front of jaws. Fingers subequal in length, claws nearly straight. Small soft crest at back of head, throat pouch, no feathers preserved on limited areas of smooth, unscaly skin.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Central Spain; Calizas de la Huérgina.
HABITS Teeth may have been for cutting plants and/or filtering small organisms, throat pouch may have been for containing fish. Hornlets and crest for display within the species.
NOTES Found as drift in nearshore marine sediments.

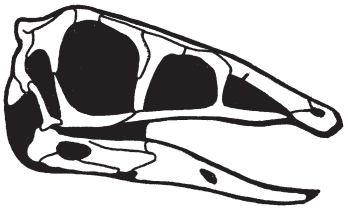
Hexing qingyi

— Adult size uncertain
FOSSIL REMAINS Complete skull and minority of skeleton, possibly immature.
ANATOMICAL CHARACTERISTICS A few small teeth at front end of lower jaw. Thumb much shorter than other fingers, claws fairly short and curved.
AGE Early Cretaceous, latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lowermost Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Shenzhousaurus orientalis

— 1.6 m (5 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS A few small, conical teeth at front end of lower jaw. Thumb not as long as other fingers, claws nearly straight.
AGE Early Cretaceous, latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

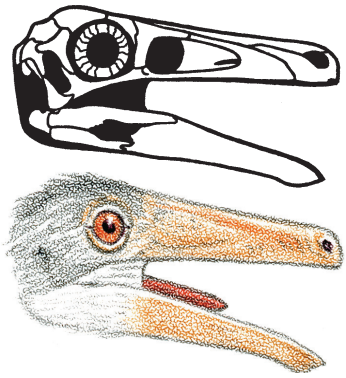
Pelecanimimus polyodon



Hexing qingyi

Harpymimus okladnikovi
— 3 m (10 ft) TL, 50 kg (110 lb)
FOSSIL REMAINS Nearly complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS A few small teeth at tip of lower jaw. Thumb not as long as other fingers, claws gently curved.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Mongolia; Shinekhudag.

Harpymimus okladnikovi



Garudimimus brevipes

Beishanlong grandis
— 7 m (23 ft) TL, 550 kg (1,200 lb)
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Fairly robustly built.
AGE Early Cretaceous, probably Aptian or Albian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.

Garudimimus brevipes
— 2.5 m (8 ft) TL, 30 kg (60 lb)
FOSSIL REMAINS Complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Toothless and beaked.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayanshiree.

Deinocheirus mirificus
— 11.5 m (38 ft) TL, 5.5 tonnes
FOSSIL REMAINS Complete skull, majority of a skeleton and minority of two others.
ANATOMICAL CHARACTERISTICS Head not as small relative to skeleton as in other ornithomimosaurs, very slender and narrow with very long beak flaring out to a small duck bill, eye sockets not large, lower jaw very

Deinocheirus mirificus

Deinocheirus mirificus

deep, jaws weakly muscled, teeth absent. Neck fairly stout. Trunk vertebrae articulated in a very strong arc up from hip and down to shoulders, vertebral spines form tall sail just in front of hips. Tail ends with a small pygostyle. Hips broader than in other ornithomimosaurs. Arm 2.5 m (9 ft) long, rather slender, fingers subequal in length, claws blunt-tipped hooks. Hip very large and deep, leg robust but not massive, foot moderately long, toes short and ending with blunt, hooflike claws.

AGE Late Cretaceous, late Campanian and early Maastrichtian?

DISTRIBUTION AND FORMATION/S Mongolia; at least lower Nemegt.

HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

HABITS That original fossil is from lower Nemegt and some others from later suggests latter remains are different species. Omnivore that fed on softer vegetation and aquatic creatures as indicated by fish remains in apparent stomach contents. Deep jaws indicate strong tongue and possible suction action. Arms could be used for gathering vegetation, possibly digging. Better able to defend itself against predators with large, clawed arms than smaller, faster ornithomimosaurs.

NOTES Examples from levels other than original fossil may be different species. Full form only recently realized from more complete remains long after discovery of isolated gigantic arms in the 1960s. This, *Beishanlong*, and *Garudimimus* may form family Deinocheiridae.

— ORNITHOMIMIDS

MEDIUM-SIZED ORNITHOMIMOSAURS OF THE CRETACEOUS, LIMITED TO THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Highly uniform. Gracile build. Toothless and beaked. Fingers subequal in length, claws at least fairly long and not strongly curved. Trunks compact. Tails shorter and lighter than standard for theropods. Pelves very large and legs very long, so leg muscles exceptionally well developed, feet very long and strongly compressed from side to side, hallux completely lost, so speed potential very high. At least some examples had large feathers on arms.
HABITS Main defense very high speed and maneuverability.
ONTOGENY Growth rates moderately rapid, adult size reached in a few years in medium-sized and large examples.
NOTES Partial remains show that some western North American examples first approached half a tonne by late Campanian.

Kinnareemimus khonkaenensis

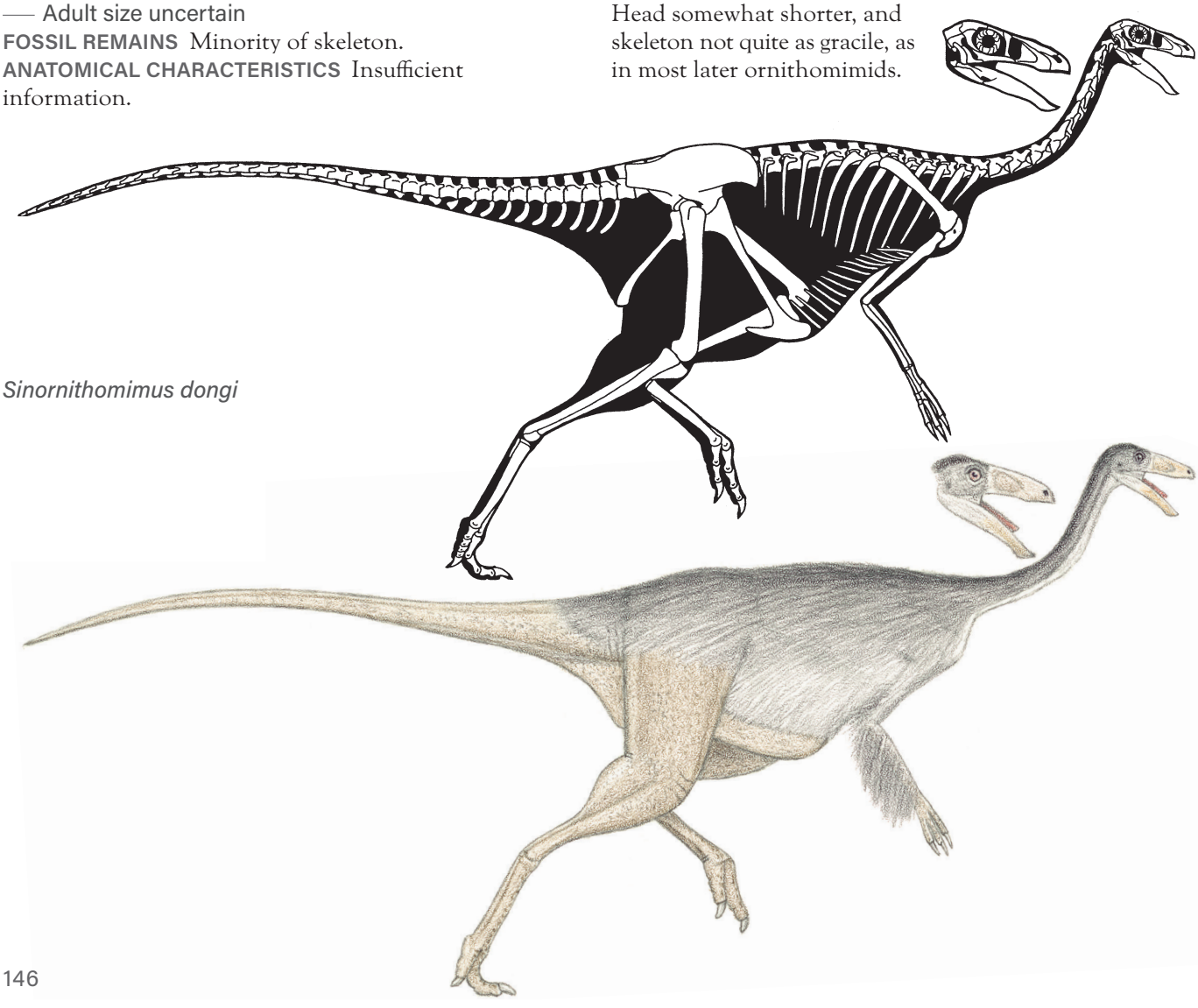
— Size not available
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Valanginian or Hauterivian.
DISTRIBUTION AND FORMATION/S Thailand; Sao Khua.

Archaeornithomimus asiaticus

— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S China; Iren Dabasu.
HABITAT/S Seasonally wet-dry woodlands.

Sinornithomimus dongi

— 2.5 m (8 ft) TL, 50 kg (110 lb)
FOSSIL REMAINS Over a dozen skulls and skeletons, many complete, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Head somewhat shorter, and skeleton not quite as gracile, as in most later ornithomimids.



Sinornithomimus dongi

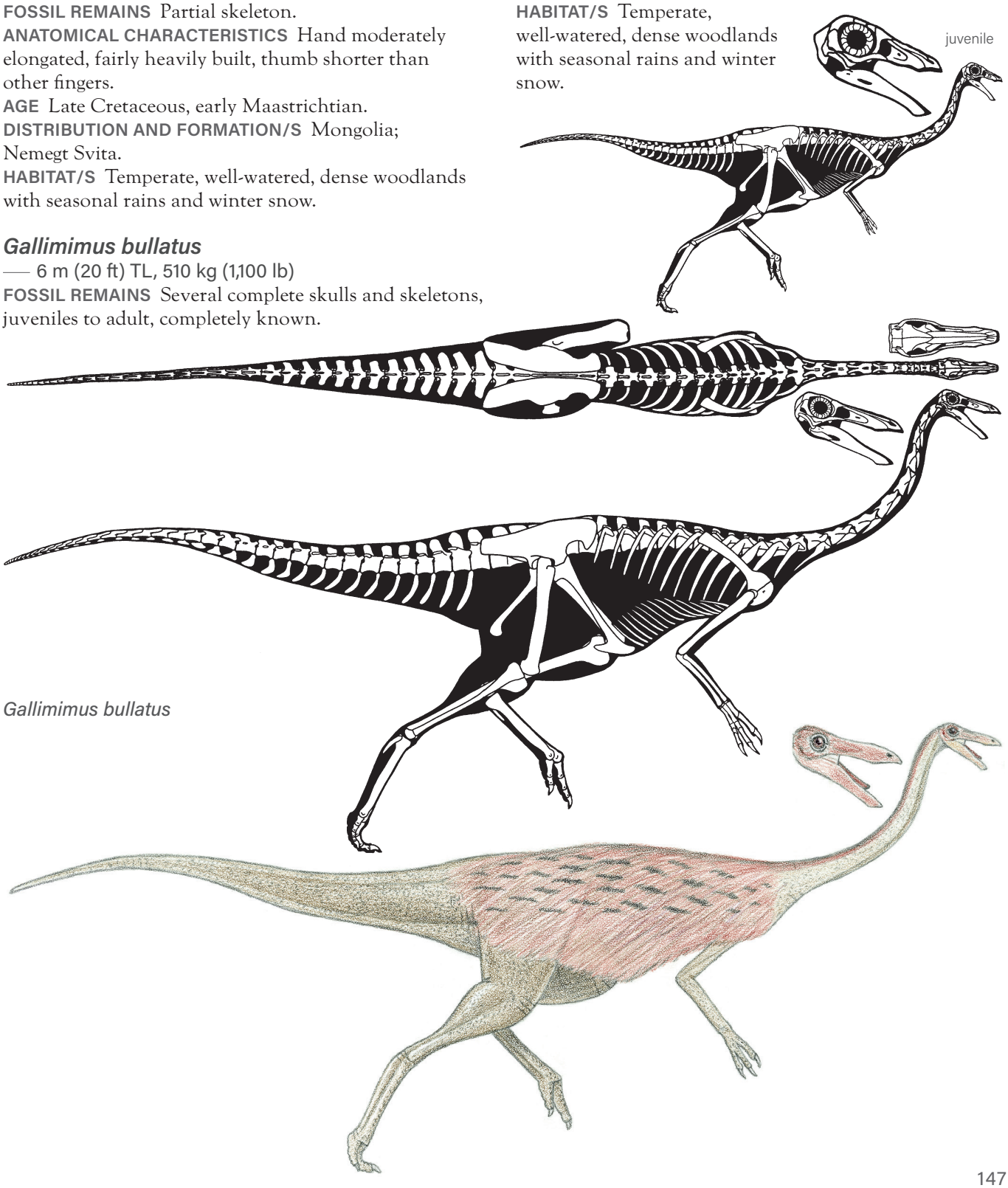
Hand elongated, thumb shorter than other fingers. Leg long.
AGE Late Cretaceous, Turonian.
DISTRIBUTION AND FORMATION/S Northern China; Ulansuhai.

Anserimimus planinychus

— 3 m (10 ft) TL, 90 kg (200 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Hand moderately elongated, fairly heavily built, thumb shorter than other fingers.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; Nemegt Svita.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

Gallimimus bullatus

— 6 m (20 ft) TL, 510 kg (1,100 lb)
FOSSIL REMAINS Several complete skulls and skeletons, juveniles to adult, completely known.
ANATOMICAL CHARACTERISTICS Beak elongated. Hand not strongly elongated, thumb shorter than other fingers, shorter armed and legged than other advanced ornithomimids.
AGE Late Cretaceous, late Campanian? and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; at least upper Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.



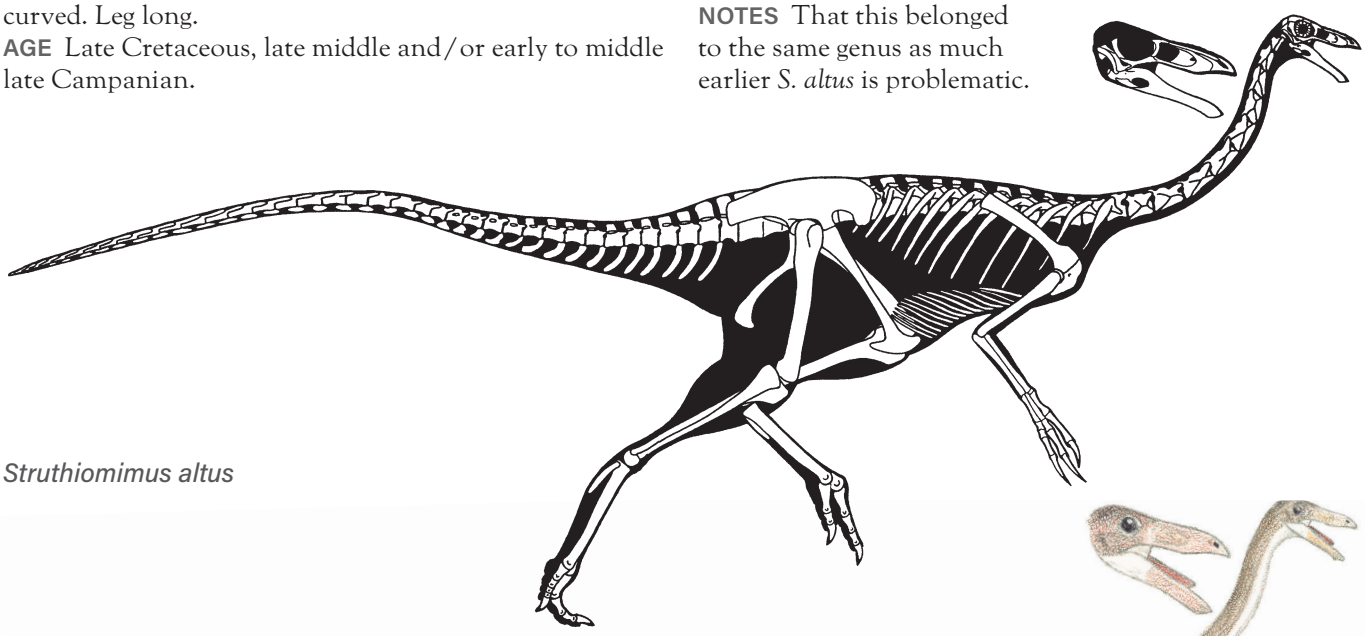
Gallimimus bullatus

HABITS Presumably not quite as swift as longer-legged ornithomimids. Suggestion that was a filter feeder because of fluted inner beak surface problematic.
NOTES That original fossil is from upper Nemegt suggests earlier remains are different species.

Rativates evadens
— 3 m (10 ft) TL, 90 kg (100 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Leg long.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Struthiomimus altus
— 4 m (13 ft) TL, 180 kg (400 lb)
FOSSIL REMAINS Several skulls and skeletons of varying completeness.
ANATOMICAL CHARACTERISTICS Hand elongated, thumb shorter than other fingers, claws fairly robust and curved. Leg long.
AGE Late Cretaceous, late middle and/or early to middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; Dinosaur Park, level uncertain.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES The adequacy of the remains that *S. altus* is based on is problematic; genus *Struthiomimus* is based on a largely complete fossil, stratigraphic levels of both are uncertain. May be an ancestor of the following *Struthiomimus* unnamed species.

Struthiomimus? unnamed species
— 4.4 m (14 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Several skulls and skeletons of varying completeness.
ANATOMICAL CHARACTERISTICS Hand elongated, thumb shorter than other fingers, claws fairly robust and curved. Leg long.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES That this belonged to the same genus as much earlier *S. altus* is problematic.



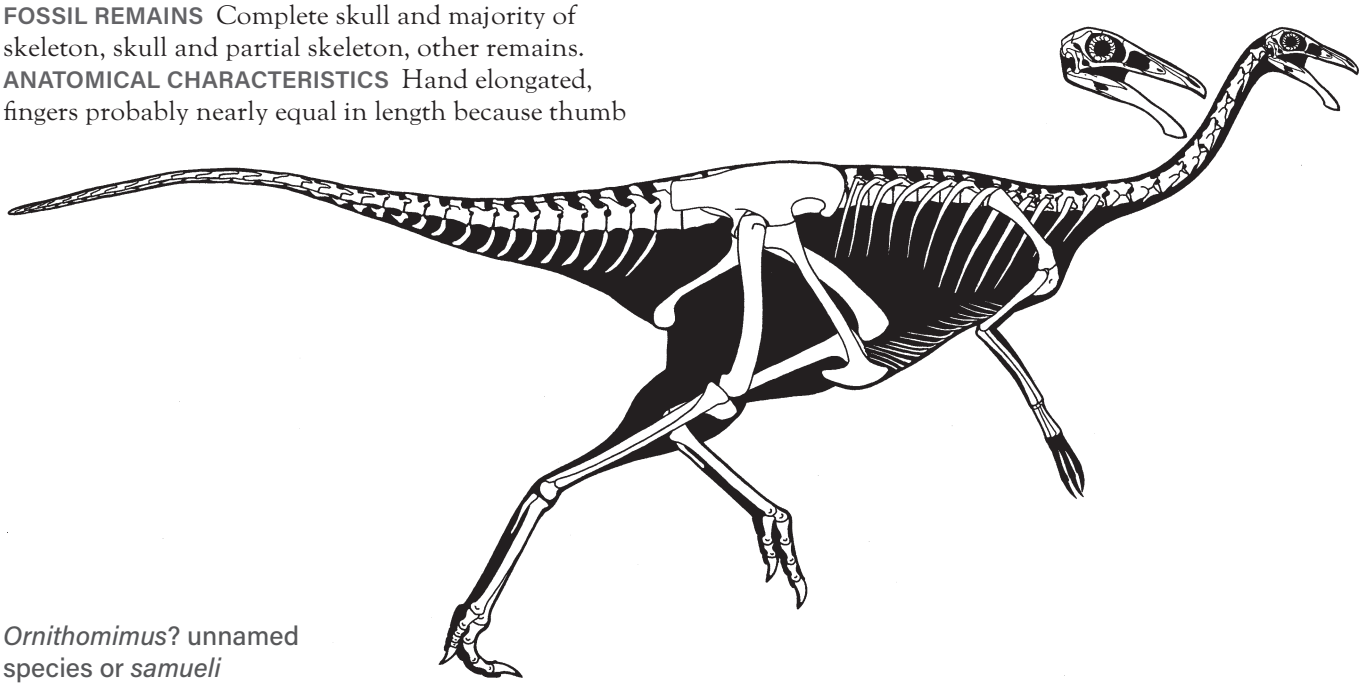
Struthiomimus altus

Ornithomimus? unnamed species or *samueli*

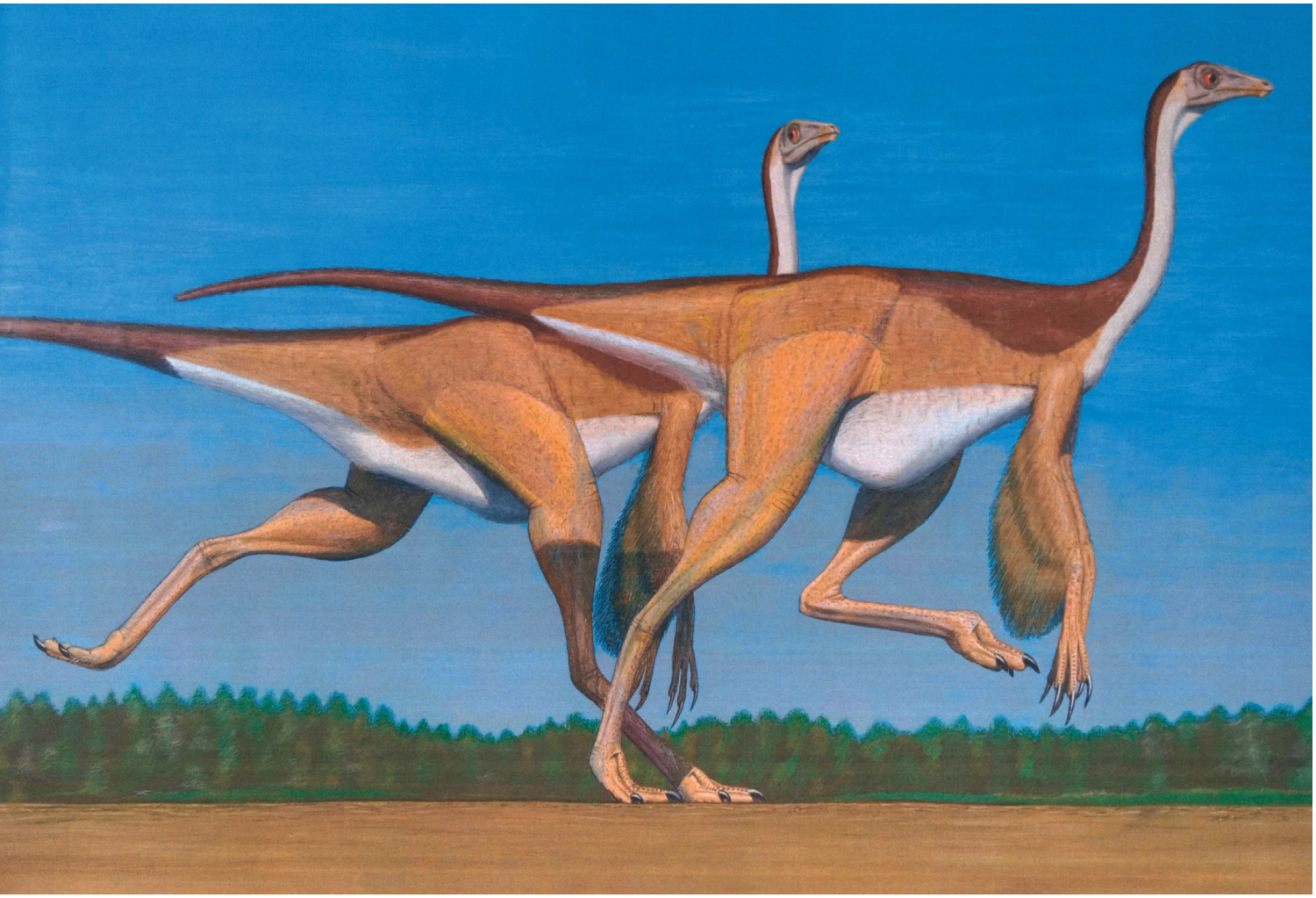
— 3.4 m (11 ft) TL, 200 kg (210 lb)

FOSSIL REMAINS Complete skull and majority of skeleton, skull and partial skeleton, other remains.

ANATOMICAL CHARACTERISTICS Hand elongated, fingers probably nearly equal in length because thumb



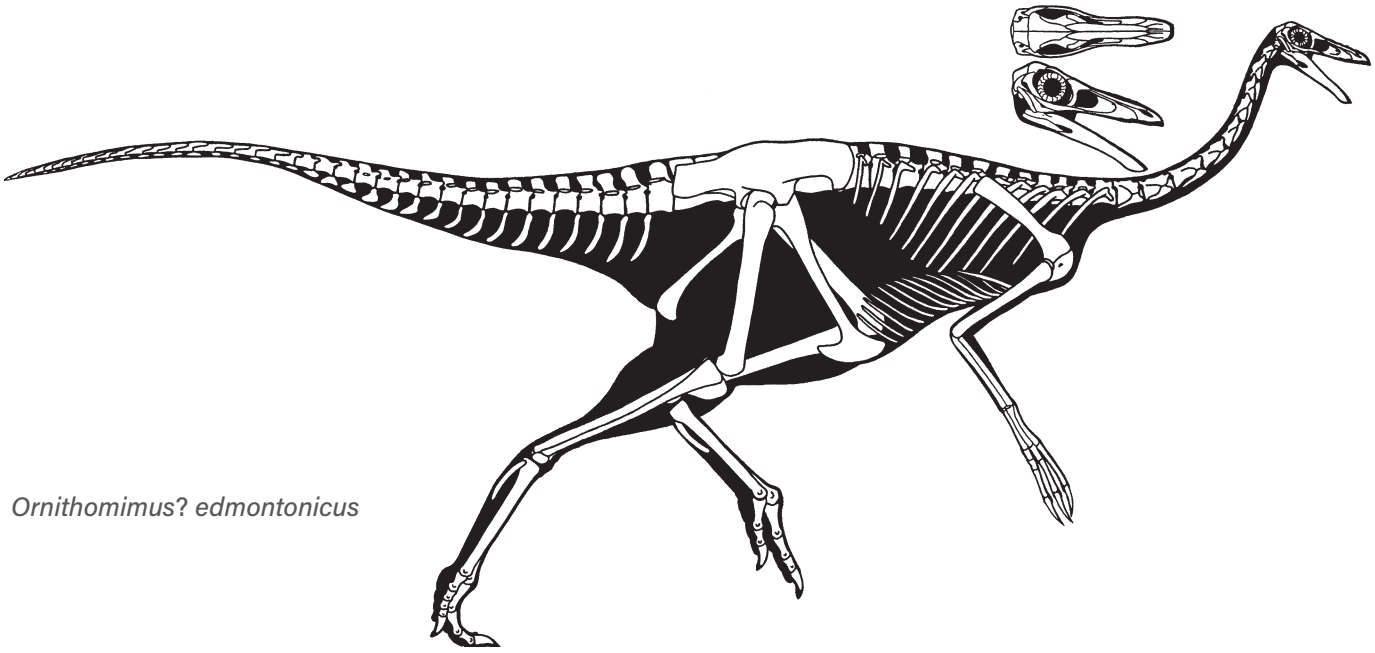
Ornithomimus? unnamed species or *samueli*



metacarpal longer than others, claws long, nearly straight, and delicate. Leg long. Short and medium-length feathers covering most of body and tail, large feathers on arm, no feathers on leg from thigh on down.
AGE Late Cretaceous, late middle and/or early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower and/or middle Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Placement in much later, more robust, fragmentary genus *Ornithomimus* problematic, as is placement in later *O.? edmontonicus* even if is in same genus. Original incomplete and damaged middle Dinosaur Park Formation *samueli* fossil may or may not be same taxon as nearly complete fossil from lower in formation. May be ancestor/s of *O.? edmontonicus*.

Ornithomimus? *edmontonicus*

— 3.8 m (16 ft) TL, 210 kg (450 lb)
FOSSIL REMAINS Skulls and skeletons of varying completeness, feathers as per prior entry.
ANATOMICAL CHARACTERISTICS Hand elongated, fingers nearly equal in length because thumb metacarpal longer than others, claws long, nearly straight, and delicate. Leg long. Short and medium-length feathers



Ornithomimus? *edmontonicus*

covering most of body and tail, large feathers on arm, no feathers on leg from thigh on down.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Usual placement in much later, more robust, fragmentary genus *Ornithomimus* problematic. Ratite-like body plumage previously predicted by this illustrator.

Ornithomimus velox
— 2.5 m (8 ft) TL, 70 kg (130 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Hand moderately elongated, fairly heavily built, fingers probably nearly equal in length because thumb base metacarpal longer than others. Leg fairly robust.
AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Colorado; upper Denver.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Presumably not quite as swift as slenderer-limbed ornithomimids.
NOTES Fossil appears to be an adult. Because is so fragmentary cannot be shown at this time that earlier ornithomimids up to 10 million years older with similar hand anatomy are in this genus. Because ornithomimids with the two types of hands with other details and otherwise very similar are found at same levels in the late Campanian and Maastrichtian of western North America, it is possible that they are the genders of the same species at a given time. If so, then *Ornithomimus* has priority over *Struthiomimus*, but the one genus lasting so long remains problematic.

Dromiceiomimus brevitertius
— 3.5 m (11.5) TL, 160 kg (350 lb)
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Leg very long because of elongated shank.
AGE Late Cretaceous, latest Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Often placed in *Ornithomimus edmontonicus* even though this species has taxonomic priority, or in genus *Dromiceiomimus* even though all western North American Campanian-Maastrichtian ornithomimids show limited variation at species level. If is a gender dimorph of contemporary *O.? edmontonicus*, then this taxon's name has priority at least at species level, and perhaps at genus level for former, and all "*Ornithomimus*" prior to latest Maastrichtian. May be direct ancestor of *D. ingens*.

Dromiceiomimus ingens
— 3.6 m (11.5) TL, 165 kg (360 lb)
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Leg very long because of elongated shank.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; upper Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Usual placement in similar but earlier *D. brevitertius* problematic. May not be smaller than other western North American ornithomimids.

Dromiceiomimus? or *Struthiomimus*? unnamed species
— 5 m (16 ft) TL, 400 kg (800 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Hand elongated, thumb shorter than other fingers, claws fairly robust and curved. Leg long because of elongated shank.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming; lower Lance.
HABITAT/S Well-watered coastal woodlands.
NOTES Usual placement of fossil in very fragmentary *Struthiomimus sedens* of unknown level of Lance is problematic, as is placement in much earlier genus, placement in somewhat earlier *Dromiceiomimus* less so, length of shank relative to femur is near boundary of two genera for a large animal.

— AIRFOILANS

SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS NEOCOELUROSAURS OF THE MIDDLE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Brains expanding and becoming more avian in form. Wrist flexion increased.
NOTES Airfoilans are neocoelurosaurs with forelimb-borne airfoils of some form, or ancestors with same that are in the clade that includes extant birds. Broadly similar but not identical to inconsistently defined maniraptors and paravians.

— SCANSORIOPTERYGIDS

SMALL AIRFOILANS OF THE MIDDLE/LATE JURASSIC OF ASIA.

ANATOMICAL CHARACTERISTICS Heads short and broad, lower jaws shallow, a few procumbent, pointed teeth at front of jaws. Necks medium length. Trunks unusually shallow because pubes quite short. Tails not very long, very abbreviated in at least some adults. Small ossified sternal plate present in at least some examples. Arms and hands elongated, hands strongly asymmetrical because outer finger is a hyperelongated, extra-lateral, very elongated strut in at least some examples, arms and hands appear to support wing membranes, finger claws large. Pelves shallow, at least in juveniles, legs not elongated, hallux partly reversed.
HABITS Very probably strongly arboreal, trunk hugging facilitated by flattened trunk. Some form of flight, at least gliding or possibly marginally powered, apparently present. Probably insectivorous.
NOTES Relationships with other neocoelurosaurs uncertain. Close relationship with oviraptorosaurs may be contradicted by presence of long tail in some examples. Appears to have been a brief evolutionary experiment in dinosaur flight that lost out to the birdlike aveairfoilans, the earliest known examples of which—*Anchiornis*, *Eosinopteryx*, *Serikornis*, and *Xiaotingia*—lived in the same habitat.

Scansoriopteryx heilmanni

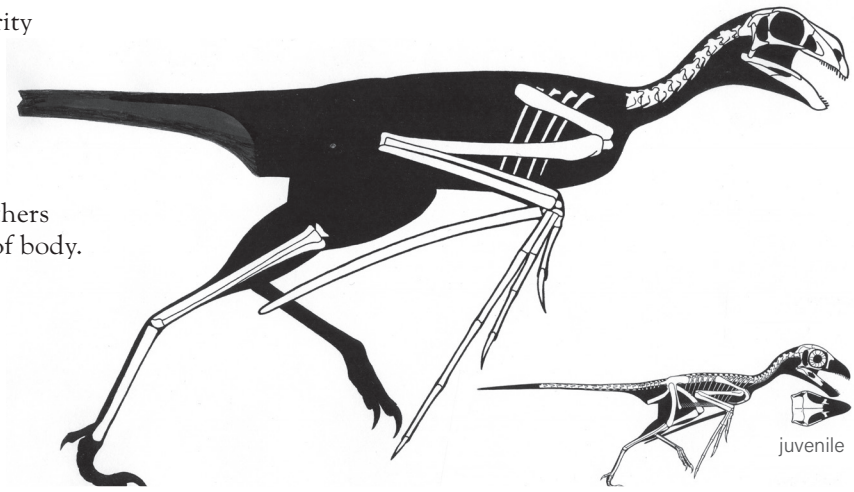
— 0.5 m (1 ft) TL, 0.17 kg (0.4 lb)
FOSSIL REMAINS Probably minority of an adult, and majority of two juvenile skeletons, all with complete or partial skulls, some feather fibers.
ANATOMICAL CHARACTERISTICS Shallow midline crest on snout, teeth small. Tail not abbreviated at least in juveniles. Arm and hand highly elongated, extra strut present in hand.
AGE Late Jurassic, middle Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Tiaojishan.
NOTES The name *Scansoriopteryx* appears to have edged out *Epidendrosaurus ningchengensis* in the race for priority. *Yi qi*—the shortest dinosaur name—is probably the adult form of this species. Lack of preserved extra hand strut in juveniles may be due to lack of sufficient growth and/or ossification. Competes with *Ambopteryx*, *Anchiornis*, *Caihong*, *Epidexipteryx*, and *Serikornis* for title of smallest known nonavian dinosaur; four of the contenders lived in the same formation.

Epidexipteryx hui

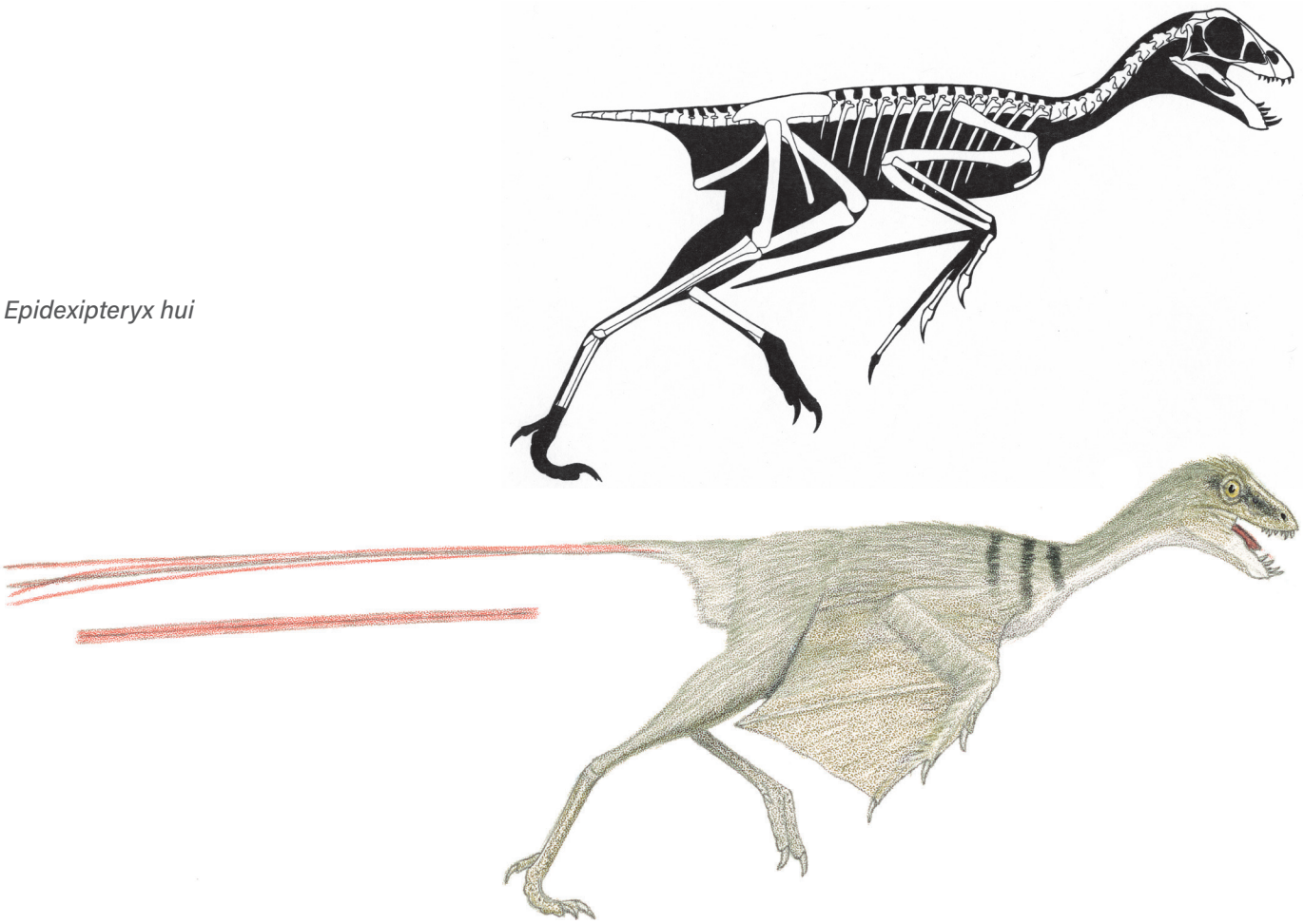
— 0.3 m (1 ft) TL, 0.25 kg (0.5 lb)
FOSSIL REMAINS Complete skull and majority of skeleton, some feather fibers.
ANATOMICAL CHARACTERISTICS Teeth of lower jaw large and procumbent. Tail abbreviated. Small ossified sternal plates present. Pubis not retroverted. Arm feathers apparently short, four very long banded feathers trail from tail, simpler feathers cover much of body.
AGE Middle or Late Jurassic, Callovian or Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; Tiaojishan.
HABITAT/S Well-watered forests and lakes.
HABITS Long tail feathers for display within the species.
NOTES Smaller wing suggests lesser flight performance than in *Scansoriopteryx* and *Ambopteryx*. Had probably the shortest known tail among nonavian dinosaurs.

Ambopteryx longibrachium

— 0.3 m (1 ft) TL, 0.25 kg (0.5 lb)
FOSSIL REMAINS Complete skull and skeleton, some feather fibers and other soft tissues.
ANATOMICAL CHARACTERISTICS Tail abbreviated, ending in slender pygostyle. Arm and hand highly elongated, extra strut present in hand. Pubis probably retroverted.
AGE Late Jurassic, Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yanliao.
HABITAT/S Well-watered forests and lakes.
NOTES Skull too damaged to restore.



Scansoriopteryx heilmanni



Epidexipteryx hui

— AVEAIRFOILANS

SMALL TO GIGANTIC PREDATORY AND HERBIVOROUS AIRFOILANS OF THE LATE JURASSIC TO THE MODERN ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Highly variable. Heads toothed to toothless and beaked; when teeth are present, serrations tend to be reduced in some manner or absent. Tails very long to very short. Shoulder girdles usually birdlike, with slender horizontal scapula blades and vertical coracoids with outer surface facing forward, furculas often large, arms very long to short, wrists usually with a large, half moon–shaped semilunate carpal block that allowed arms to be more folded, hands usually long. Brains enlarged, semiavian in form. Pennaceous feathers often present. Overall appearance usually very birdlike.
ONTOGENY Growth rates apparently moderate.
HABITS Reproduction generally similar to that of ratites and tinamous; in at least some cases males incubated the eggs and were probably polygamous; egg hatching in a given clutch not synchronous.
NOTES Aveairfoilans are airfoilans with avian shoulder girdles, or ancestors with same that are in the clade that includes extant birds. Prone to evolving and especially losing flight, perhaps repeating cycle in some cases.

— AVEAIRFOILAN MISCELLANEA

Yixianosaurus longimanus

— 1 m (3 ft) TL, 1 kg (2.2 lb)
FOSSIL REMAINS Arms.
ANATOMICAL CHARACTERISTICS Hands elongated, finger claws large and strongly hooked.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian.

HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Well-developed arms suitable for handling prey and climbing.
NOTES Relationships very uncertain, may not be aveairfoilan.

Balaur bondoc
— 2.5 m (9 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Robustly built. Upper hand elements fused, outer finger very reduced. Pubis very retroverted, foot short, broad, inner toe large so foot effectively tetradactyl, inner two toes hyperextendable with large claws.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Romania; Sebeş.
HABITAT/S Forested island.
HABITS Probably secondarily flightless. Possibly omnivorous or herbivorous, in which case double sickle claws used for defense and climbing rather than primarily for predation.
NOTES Originally thought to be a predatory dromaeosaur, more probably a near-bird.

— DEINONYCHOSAURS

SMALL TO MEDIUM-SIZED PREDATORY AND OMNIVOROUS AVEAIRFOILANS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, ON MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly variable. Eyes face partly forward and some degree of stereo vision possible, tooth serrations reduced or absent. Tails slender, bases very flexible, especially upward. Arms and hands well developed, sometimes very long, finger claws large hooks. Second toe hyperextendable and/or claw at least somewhat enlarged.
HABITS Very agile, sophisticated predators and omnivores, prey varying from insects and small game to big game. Climbing ability generally good, especially in smaller species, longer-armed species, and juveniles; hyperextendable toe could be used as hook and spike during climbing in species living in areas with trees. Second toe claw used as weapon to dispatch prey—especially when claw and species it was borne by were large—to pin down prey, and in defense. Two-toed trackways confirm that hyperextendable claw was normally carried clear of ground; relative scarcity of such trackways indicates most deinonychosaurs did not spend much time patrolling shorelines.
NOTES Is not known whether deinonychosaurs were a distinct group or a stage within aveairfoilans, membership also uncertain. Presence of large sternal plates, ossified sternal ribs, and ossified uncinate processes in most flightless deinonychosaurs indicates they were secondarily flightless.

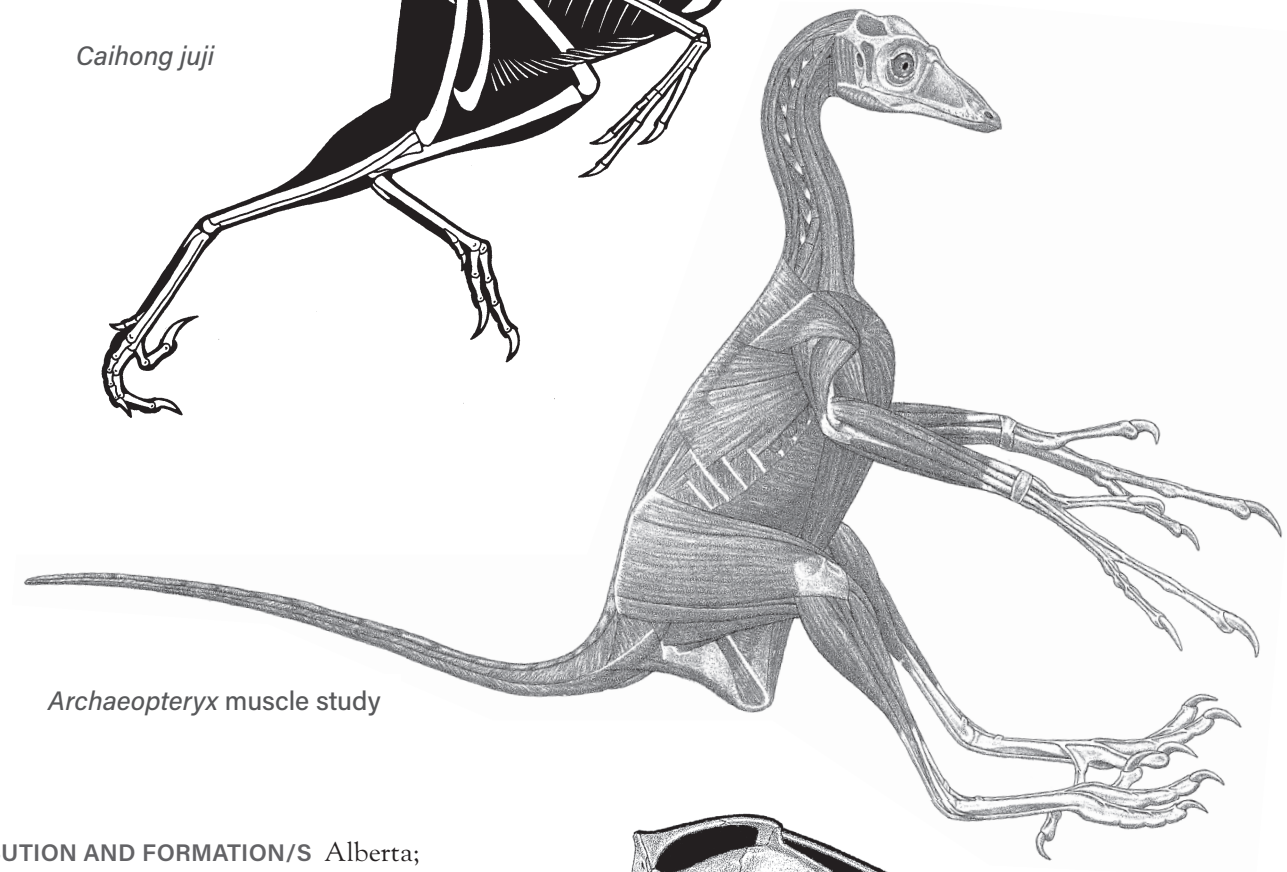
— DEINONYCHOSAUR MISCELLANEA

NOTES: Neither the placement of these aveairfoilans in the deinonychosaurs nor their placement within the group is certain.

Caihong juji
— 0.4 m (1.3 ft) TL, 0.3 kg (0.7 lb)
FOSSIL REMAINS Complete skull and skeleton, significantly damaged, extensive feathers.
ANATOMICAL CHARACTERISTICS Head long, shallow, subrectangular; apparent long, low, paired crests atop snout, teeth fairly large, bladed. Tail medium length. Arm much shorter than leg. Pubis long and vertical. Toe claws not strongly curved. Well-developed head feather crest, arm primary feathers symmetrical, moderately long on arm, same on leg, tail fan very broad and long, short feathers on toes, feathers black, also iridescent at least on head, chest, tail base.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Tiaojishan.
HABITAT/S Well-watered forests and lakes.
HABITS Bladed teeth indicate hunted fairly substantial game. Lack of strongly curved toe claws indicates was not highly arboreal. Arm wing too small and primary feathers too symmetrical for flight, at most a parachuting or very modest gliding ability was present, potentially secondarily flightless. Large tail fan primarily for display.
NOTES Size, shape, and orientation of possible snout crests and other head proportions uncertain because of distortion of preserved skull, same for skeletal details. Competes with *Ambopteryx*, *Anchiornis*, *Epidexipteryx*, *Scansoriopteryx*, and *Serikornis* for title of smallest known nonavian dinosaur; four of the contenders lived in the same formation.

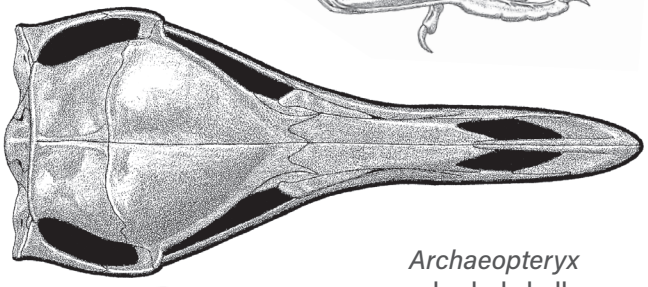
Richardoestesia (or *Ricardoestesia*) *gilmorei*
— 2 m (3.5 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Lower jaw very slender.
AGE Late Cretaceous, late middle and/or early to middle late Campanian.

Caihong juji

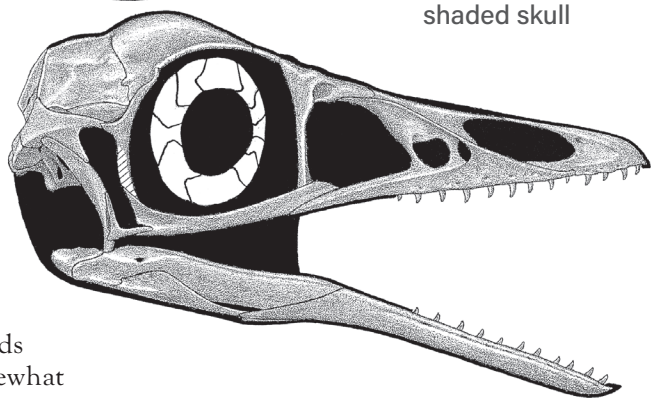


Archaeopteryx muscle study

DISTRIBUTION AND FORMATION/S Alberta; Dinosaur Park, level uncertain.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Hunted small game, fished.
NOTES May be a dromaeosaurid or troodontid. Numerous remains imply type was common in other late Late Cretaceous habitats.



Archaeopteryx shaded skull

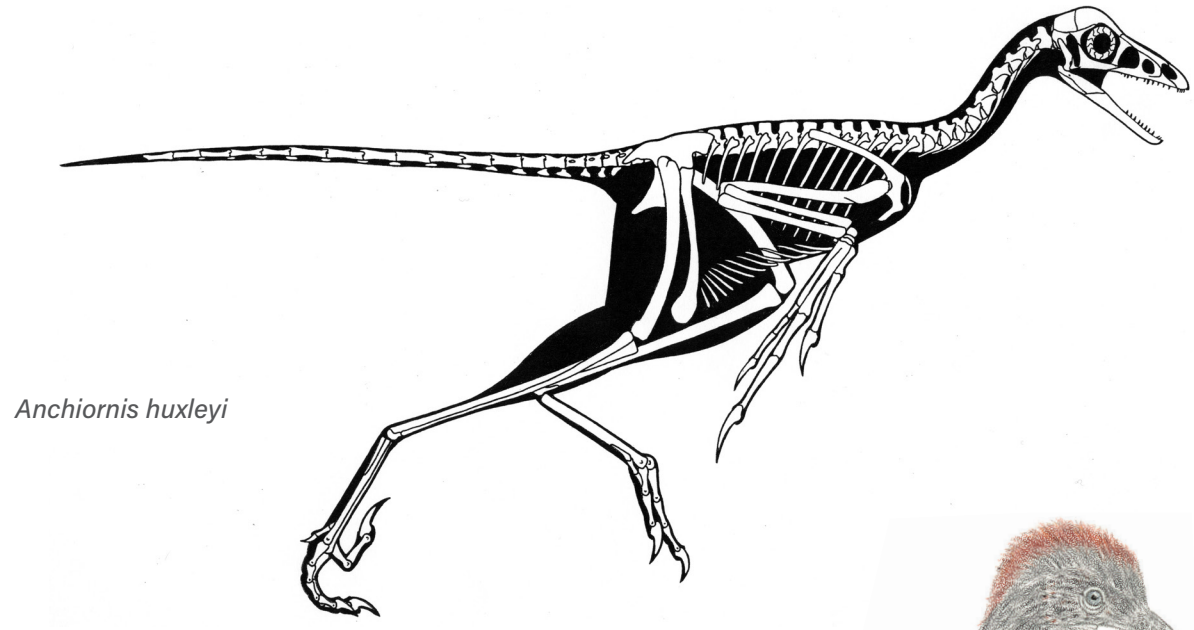


— ARCHAEOPTERYGIANS

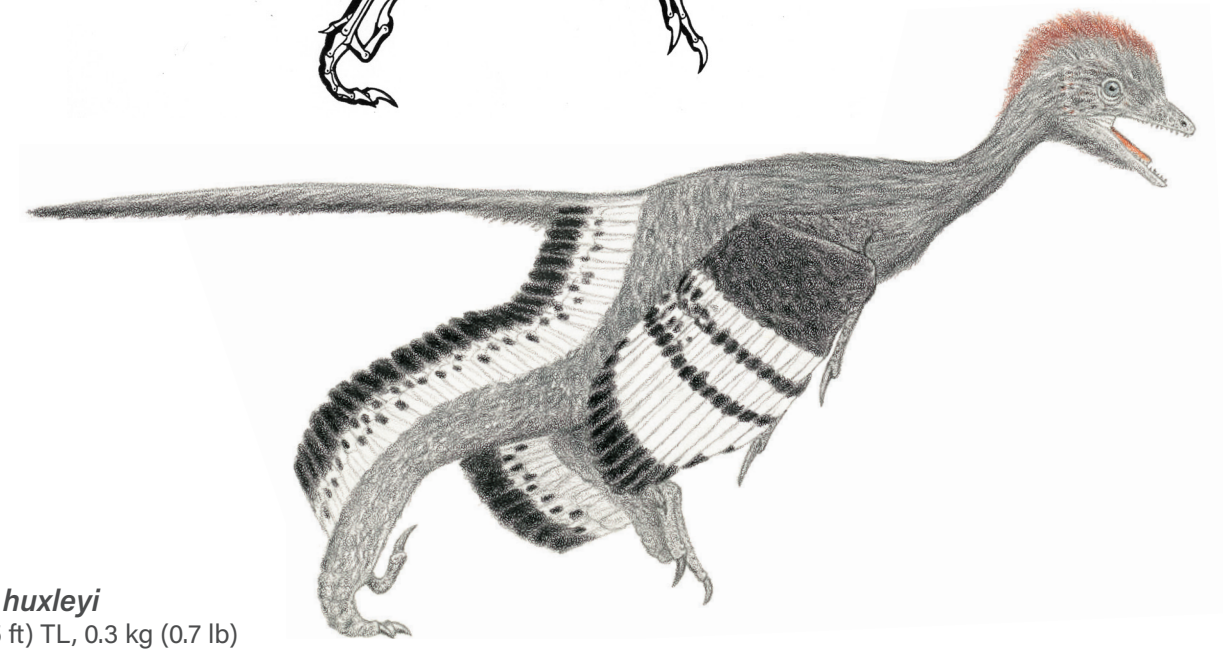
SMALL, LARGE-ARMED PREDATORY DEINONYCHOSAURS LIMITED TO THE LATER JURASSIC OF EURASIA.

ANATOMICAL CHARACTERISTICS Lightly built. Heads not large, subtriangular, teeth small, not highly numerous, unserrated. Trunks deep because pubes long and not strongly retroverted; ossified sternal plates, sternal ribs, and uncinate processes on ribs absent. Tails medium length. Arms and hands elongated. Legs elongated, second toes slender and claws somewhat enlarged, maybe hyperextendable.
HABITS Digestive tract contents confirm hunted small game and fished, first known dinosaurs to form gastric pellets. Flight performance minimal to significant.
NOTES Extent of group and relationships of these early aveairfoilans are uncertain.

Anchiornis huxleyi



Anchiornis huxleyi



Anchiornis huxleyi

— 0.5 m (1.5 ft) TL, 0.3 kg (0.7 lb)

FOSSIL REMAINS Complete skulls and skeletons, extensive feathers, gastric pellets.

ANATOMICAL CHARACTERISTICS Head short, subtriangular. Arm not as long as leg. Well-developed head feather crest, arm primary feathers symmetrical, moderately long on arm, same on leg, feather edges somewhat irregular, short feathers on toes, most feathers dark gray or black, head feathers speckled reddish brown, head crest partly brown or reddish brown, broad whitish bands on arm and leg feathers interrupted by narrow dark irregular bands, primary feather tips black.

AGE Late Jurassic, middle Oxfordian.

DISTRIBUTION AND FORMATION/S Northeastern China; middle Tiaojishan.

HABITAT/S Well-watered forests and lakes.

HABITS Arm wing too small and primary feathers too symmetrical for flight, at most a parachuting or very modest gliding ability was present, potentially secondarily flightless.

NOTES Probably includes *Aurornis xui*. May be a troodont.

Eosinopteryx brevipenna?

— 1 m (3 ft) TL, 1 kg (2.2 lb)

FOSSIL REMAINS Complete skull and skeleton, possibly juvenile, minority of skeleton, extensive feathers.

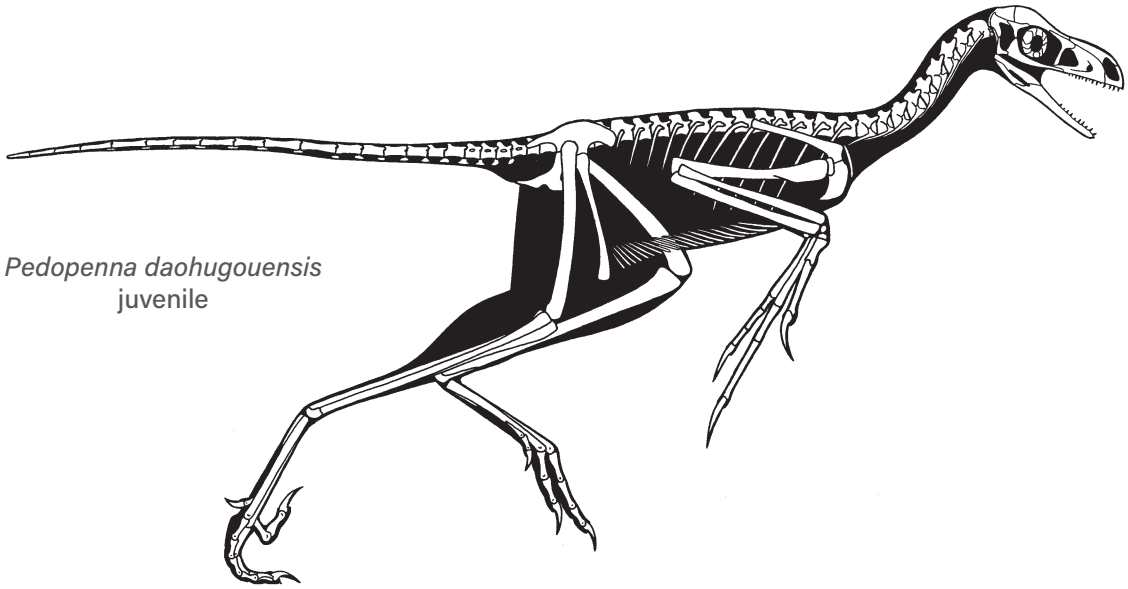
ANATOMICAL CHARACTERISTICS Head short, subrectangular. Arm not as long as leg. Toe claws not strongly curved, claw on second toe markedly larger than others. Primary feathers on arm symmetrical, may be symmetrical pennaceous feathers on upper foot, feather edges somewhat irregular.

AGE Late Jurassic, middle Oxfordian.

DISTRIBUTION AND FORMATION/S Northeastern China; middle Tiaojishan.

HABITAT/S Well-watered forests and lakes, winters chilly with snow.

HABITS Not highly arboreal. Arm wing too small and primary feathers too symmetrical for flight, absence of tail feathers indicates same, at most a parachuting ability was present, potentially secondarily flightless.



Pedopenna daohugouensis
juvenile

NOTES May be the juvenile of *Pedopenna daohugouensis* if from same middle level of formation. May be an anchiornid or troodont. If not a juvenile, is among smallest known dinosaurs.

Serikornis sungei

— 0.5 m (1.5 ft) TL, 0.2 kg (0.5 lb)
FOSSIL REMAINS Complete badly damaged skull and skeleton, extensive feathers.
ANATOMICAL CHARACTERISTICS Head short, probably subtriangular. Neck fairly long, tail long. Arm shorter than leg. Primary feathers on arm symmetrical, pennaceous feathers apparently absent on leg and tail, short feathers on toes.
AGE Late Jurassic, Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; Tiaojishan.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.
HABITS Arm wing too small and primary feathers too symmetrical for flight, absence of tail feathers indicates same, at most a parachuting ability was present, potentially secondarily flightless.
NOTES Damage to skull precludes skeletal restoration. May be an anchiornid or troodont. Competes with *Ambopteryx*, *Anchiornis*, *Caihong*, *Epidexipteryx*, and *Scansoriopteryx* for title of smallest known nonavian dinosaur; four of the contenders lived in the same formation.

Xiaotingia zhengi

— 0.6 m (2 ft) TL, 0.6 kg (1.4 lb)
FOSSIL REMAINS Majority of skull and skeleton, poorly preserved feathers.
ANATOMICAL CHARACTERISTICS Head short, subtriangular, teeth blunt. Arm not as long as leg. Toe claws strongly curved. Long pennaceous feathers on leg, otherwise preservation of feathers insufficient for assessment.
AGE Late Jurassic, Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; Tiaojishan.
HABITS Strongly arboreal. Arm wing too small for significant flight, at most a parachuting ability was present, potentially secondarily flightless.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.
NOTES May be a dromaeosaur or troodont, or the closest known relative of *Archaeopteryx*.

Ostromia crassipes

— 0.4 m (1.3 ft) TL, 0.55 m (1.8 ft) wingspan, 0.5 kg (1.1 lb)
FOSSIL REMAINS Minority of skeleton (Haarlem), with feathers.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, earliest? Tithonian.
DISTRIBUTION AND FORMATION/S Southern Germany; middle? Painten.
HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.
NOTES Long placed in *Archaeopteryx*, which it shared its habitat/s with, but now considered more basal. Indicates Solnhofen protobird fauna more diverse than previously realized, as does the more advanced flier *Alcmonavis*.

Archaeopteryx siemensii

— 0.4 m (1.3 ft) TL, 0.55 m (1.8 ft) wingspan, 0.23 kg (0.5 lb)
FOSSIL REMAINS Two nearly complete skulls and skeletons (Berlin, Schamhaupten), at least some immature, extensive feathers, nearly completely known.

ANATOMICAL CHARACTERISTICS Head subtriangular, snout pointed, teeth subconical, unserrated. Trunk shallower because pubis more retroverted. Tail modest in length. Arm longer and more strongly built than leg. Hallux fairly large and semireversed, toe claw curvature modest at least in juveniles. Most of body covered by short feathers, arm and hand supporting well-developed, broad chord wings made of asymmetrical, crisp-edged feathers. Lower leg supporting a modest-sized feather airfoil, tail supporting a long set of feather vanes forming an airfoil.

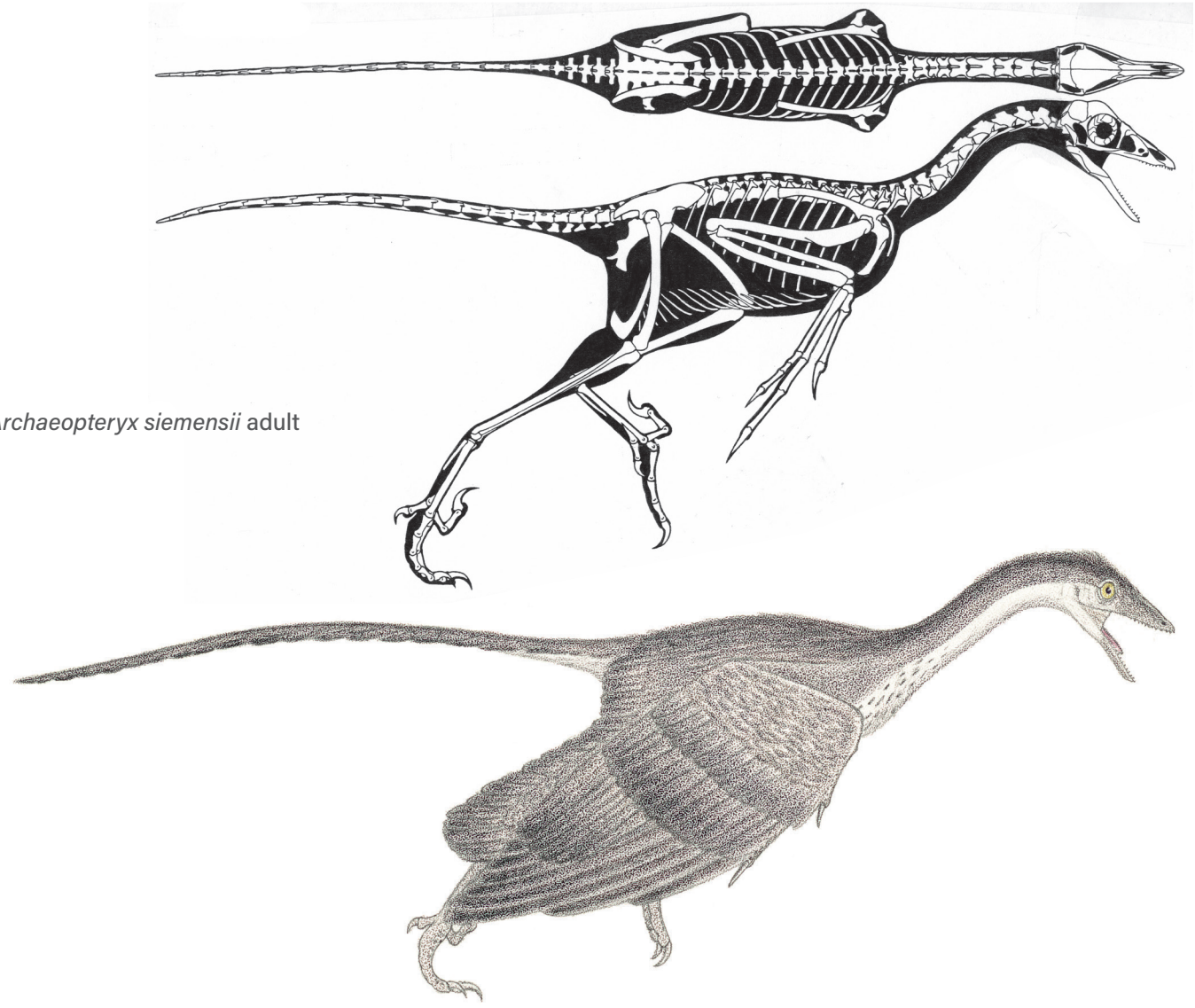
AGE Late Jurassic, middle Kimmeridgian.

DISTRIBUTION AND FORMATION/S Southern Germany; lowermost Altmühltal, lowermost Painten.

HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.

HABITS Probably semiarboreal. Capable of low-grade powered flight and gliding probably somewhat inferior to that of *Sapeornis*, immature condition of fossils may be leading to underestimation of flight abilities because adult wing elements may have been more fused, etc. Legs could not splay out nearly flat so feathers probably used as auxiliary rudders and air brakes. May have been able to swim with wings. Defense included climbing and flight, and claws.

NOTES Long known as the first bird, "Urvogel," *Archaeopteryx* is now known to be one among an array of later Jurassic dinobirds. Fossils placed in genus span over 1.5 million years and are unlikely to be one or two species, of which *A. lithographica* has priority, that last most or all of that time; species may have appeared in stratigraphic sequence but multiple species at a given time are possible, and/or some species may have been present for somewhat longer time than presented here. *A.siemensii* is best-preserved species. Some contend that all fossils are juveniles and that maximum mass was over 25 percent heavier. This genus and *Xiaotingia* may form family Archaeopterygidae. May be direct ancestor of *A.grandis*.



Archaeopteryx siemensii adult

Archaeopteryx grandis

— 0.5 m (1.7 ft) TL, 0.7 m (2.3 ft) wingspan, 0.45 kg (1 lb)

FOSSIL REMAINS Several skulls and skeletons of varying completeness (Solnhofen, Thermopolis, Altmühl, Eichstätt), at least some immature, extensive feathers.

ANATOMICAL CHARACTERISTICS Largely same as for *A. siemensii*. Toe claw curvature modest at least in juveniles.

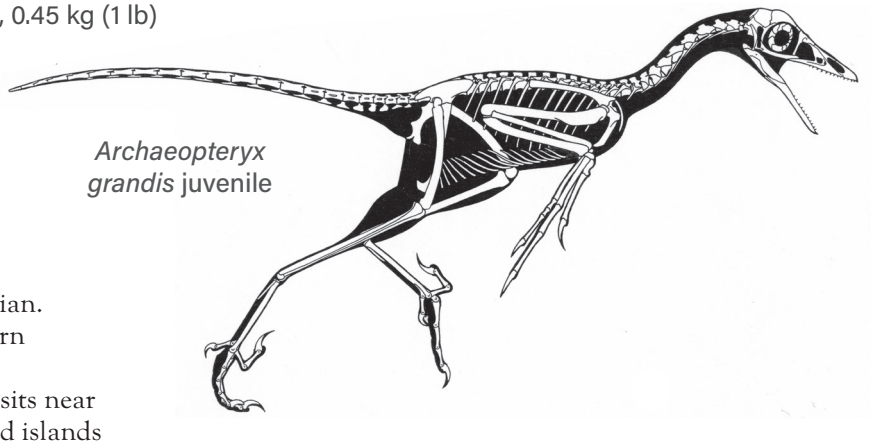
AGE Late Jurassic, latest middle Kimmeridgian.

DISTRIBUTION AND FORMATION/S Southern Germany; middle Altmühltal.

HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.

HABITS Largely same as for *A. siemensii*.

NOTES Placement in genus *Wellnhoferia* problematic, *A.recurva* is probably the juvenile of this species. Unusual fourth toe of Solnhofen fossil probably individual anomaly. May be direct ancestor of *A. lithographica*.



Archaeopteryx grandis juvenile

Archaeopteryx lithographica

— 0.45 m (1.5 ft) TL, 0.6 m (2 ft) wingspan, 0.34 kg (0.75 lb)

FOSSIL REMAINS Several partial skulls and skeletons (London, Munich, Maxberg), at least some immature, extensive feathers.

ANATOMICAL CHARACTERISTICS Largely same as for *A.siemensii*. Toe claw curvature strong at least in some adults.

AGE Late Jurassic, earliest late Kimmeridgian.

DISTRIBUTION AND FORMATION/S Southern Germany; upper Altmühltal.

HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.

HABITS Largely same as for *A. siemensii*.

NOTES Original fossil is a feather that may or may not be the same taxon as the skeletons from this same level; feather color patterns restored for this species based on feather correspondingly problematic, more so for other *Archaeopteryx* species. Probably includes *A. bavarica*. May be direct ancestor of *A. albersdoerferi*.

Archaeopteryx or unnamed genus *albersdoerferi*

— 0.35 m (1.7 ft) TL, 0.7 m (2.3 ft) wingspan, 0.15 kg (0.35 lb)

FOSSIL REMAINS Partial skull and skeleton (Daiting), probably adult.

ANATOMICAL CHARACTERISTICS Extensive fusion of various elements.

AGE Late Jurassic, middle late Kimmeridgian.

DISTRIBUTION AND FORMATION/S Southern Germany; Mörnsheim, level uncertain.

HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.

HABITS Extensive fusion of wrist and upper hand suggests superior flight abilities or is an adult feature.

NOTES May not belong to earlier *Archaeopteryx*.

— ALCMONAVIANS

SMALL POSSIBLE DEINONYCHOSAURS OF THE LATE JURASSIC OF EUROPE.

ANATOMICAL CHARACTERISTICS Central finger bases flattened to better support fully developed, broad chord wings.

NOTES Relationships uncertain, may not be deinonychosaurs, may be basal birds.

Alcmonavis poeschli

— 0.6 m (2 ft) TL, 0.8 m (2.8 ft) wingspan, 0.8 kg (1.7 lb)

FOSSIL REMAINS Minority of skeleton (Mühlheim).

ANATOMICAL CHARACTERISTICS As for group.

AGE Late Jurassic, middle late Kimmeridgian.

DISTRIBUTION AND FORMATION/S Southern Germany; lower Mörnsheim.

HABITAT/S Found as drift in lagoonal deposits near probably arid, brush- and mangrove-covered islands then immediately off the northeastern coast of North America.

HABITS Markedly better-powered flier than contemporary *Archaeopteryx.*

NOTES Earliest known dinosaur with a flattened finger base for an improved outer wing.

— DROMAEOSAURIDS

SMALL TO MEDIUM-SIZED FLYING AND FLIGHTLESS PREDATORY DEINONYCHOSAURS OF THE CRETACEOUS, ON MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly variable. Teeth bladed, serrations limited to back edge, quadratojugal usually inverted T shape. Neck ribs so short they do not overlap, increasing flexibility of neck. Arms large to very large. Tails usually long to very long and ensheathed in very long and slender ossified tendons. Large ossified sternal plates, sternal ribs, and uncinate processes present. Large sickle claws on robust hyperextendable toes. Olfactory bulbs enlarged.
HABITS Archpredators equipped to ambush, pursue, and dispatch relatively large prey using sickle claw as a primary weapon, especially when large and borne by large species, as well as to pin down prey. Sickle claw also facilitated climbing taller prey. Leaping performance when arboreal or attacking prey excellent. Flight performance from well developed to none; the retention of the pterosaur-like ossified tendons in flightless dromaeosaurids is further evidence that they were secondarily flightless. Juveniles of large species with longer arms may have possessed some flight ability.
NOTES Teeth imply that small members of the group may have evolved by the Late Jurassic. Fragmentary remains indicate presence in Australia.

— MICRORAPTORINES

SMALL FLYING DROMAEOSAURIDS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

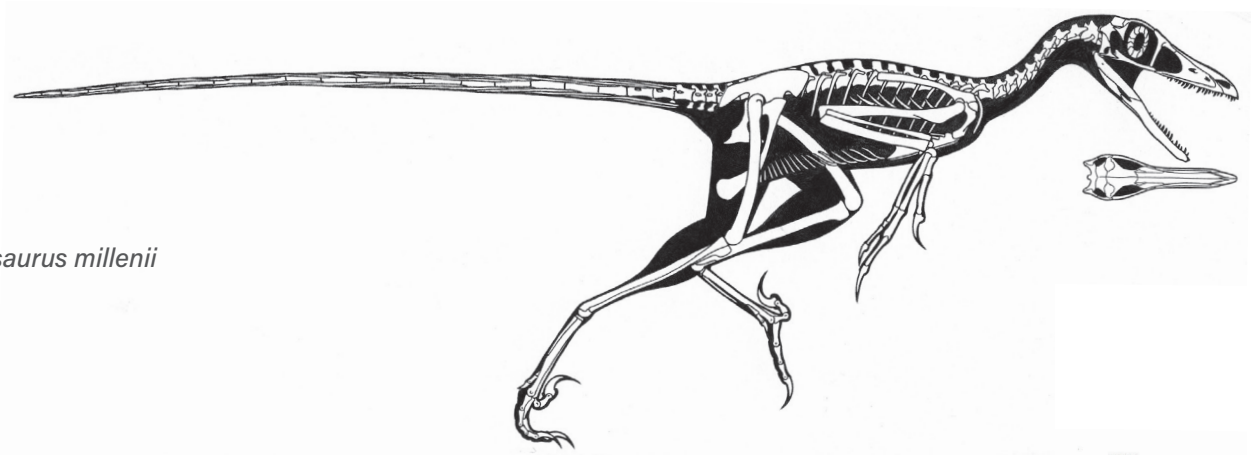
ANATOMICAL CHARACTERISTICS Lightly built. Tooth serrations reduced in various ways. Arms and hands very large, outer, upper hand bone curved, central fingers stiffened and bases flattened to better support fully developed, broad chord wings made of asymmetrical crisp-edged eathers. Hip sockets more upwardly directed than usual, legs very long, supported well-developed second wing made of asymmetrical feathers that extended onto upper foot, head of femur more spherical than in other theropods, sickle claws well developed, other toe claws strongly curved. Part of heads and most of bodies covered by short, simple feathers, tails supported a long set of feather vanes, forming an airfoil.
HABITAT/S Well-watered forests and lakes.
HABITS Very large, stiff foot feathers not well suited for running, and strongly curved toe claws indicate strong arboreality. Better development of sternum, sternal ribs, and uncinates, more streamlined trunks, modified upper hands and central fingers, larger outer arm wings, extra leg wings, and pterosaur-like tails indicate microraptorines were better-powered fliers than *Archaeopteryx* and *Sapeornis*. Leg appears to have been more splayable sideways than normal in theropods because hip sockets face more upward, femoral heads are more spherical, and legs are often splayed sideways in articulated fossils (unlike most articulated theropods, including *Archaeopteryx*, which are usually preserved on their sides), but hind wings were not flappable and possibly provided extra wing area during glides or soaring, and air brakes when landing or ambushing prey from the air.
NOTES Similar limb design indicates all microraptorines had forewings and hind wings, preserved only in *Sinornithosaurus zhaoianus* (wing feathers are missing from a number of other Yixian bird species). *Zhongjianosaurus yangi* and *Shanag ashile* may be basal birds. The limitation of these basal dromaeosaurids to the Northern Hemisphere may reflect lack of sufficient sampling.

Sinornithosaurus (or *Graciliraptor*) *lujiatunensis*

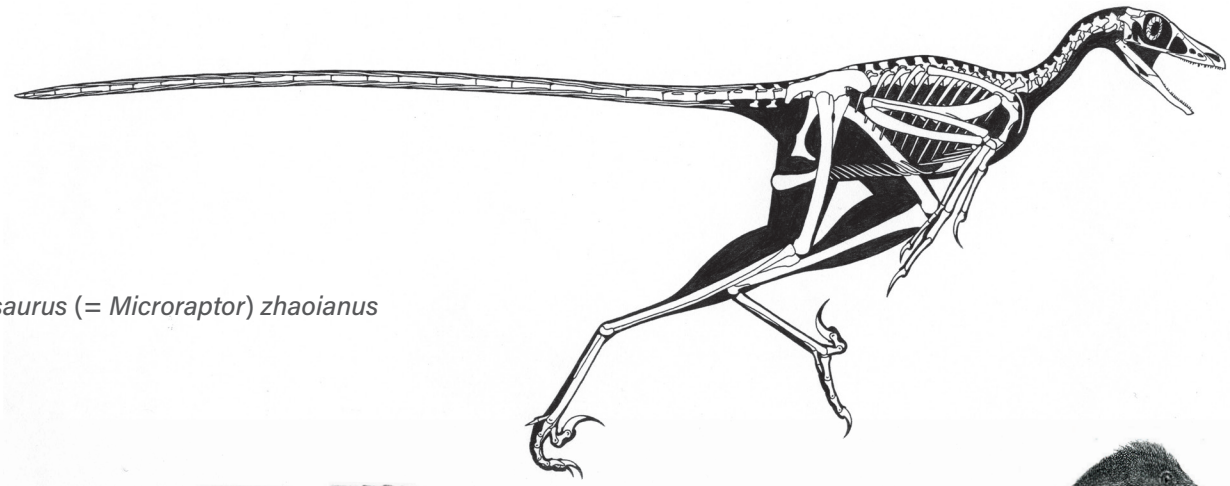
— 1 m (3 ft) TL, 1.5 kg (3.5 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Hand slender.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lowermost Yixian.
HABITAT/S Placement in distinct genus problematic. Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Sinornithosaurus millenii

— 1.2 m (4 ft) TL, 3 kg (6.5 lb)
FOSSIL REMAINS Nearly complete skull and majority of skeleton, poorly preserved feathers.
ANATOMICAL CHARACTERISTICS Head large, long, and shallow, jugal shallow and postorbital bar probably incomplete, quadratojugal inverted T shape with short vertical process. Trunk shallow because pubis double retroverted. Furcula and sternal plates large. Tail not very long. Feathers irregularly black and rufous.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Could hunt similarly large prey.
NOTES Poor preservation of feathers has caused many to problematically presume it was not winged despite flattening of central finger. The genus appears to have



Sinornithosaurus millenii



Sinornithosaurus (= *Microraptor*) *zhaoianus*

OPPOSITE:
Sinornithosaurus (= *Microraptor*) *zhaoianus*

included multiple fairly similar species over millions of years from the base of the Yixian to the top of the Jiufotang formations.

Sinornithosaurus (= *Changyuraptor*) *yangi*

— 1 m (3.4 ft) TL, 2.5 kg (5 lb)
FOSSIL REMAINS Complete but poorly preserved skull and skeleton, some feathers.
ANATOMICAL CHARACTERISTICS Tail not very long, tail feathers exceptionally long. Trunk shallow because pubis double retroverted. Furcula and sternal plates large.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian, level uncertain.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Similar to *S. millenii*.
NOTES Placement in distinct genus problematic. Establishes that large microraptorines were winged fliers.

Sinornithosaurus (= *Microraptor*) *zhaoianus*

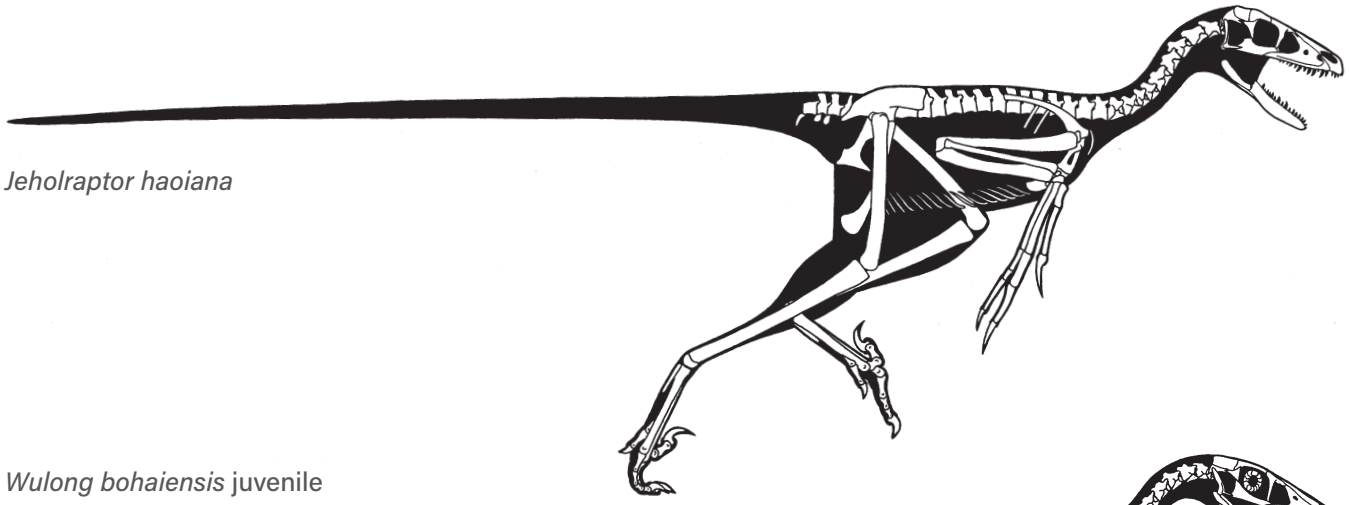
— 0.85 m (2.8 ft) TL, 0.85 m (2.8 ft) wingspan, 1 kg (2 lb)
FOSSIL REMAINS Large number of complete and partial, usually damaged skulls and skeletons, extensive well-preserved feathers, adult to juvenile.
ANATOMICAL CHARACTERISTICS Head not proportionally large, subtriangular, jugal shallow and postorbital bar probably incomplete, teeth less bladelike and less serrated than in *S. millenii*. Neck rather short, tail very long. Trunk shallow because pubis double retroverted. Furcula and sternal plates large. Leg quite long. Leg feathers preserved, overall feathers black with iridescence.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Strongly curved toe claws indicate strong arboreality. Both lesser size and less bladed and serrated teeth indicate that this attacked smaller prey than *S. millenii*; gut contents include small fish, birds, mammals.
NOTES Placement in distinct genus problematic, may include *S. gui* and *S. hanqingi*. Second only to *Sinosauropteryx* in being accurately restorable among dinosaurs, the orientation of the leg feathers posing the greatest uncertainty.

Sinornithosaurus (= *Microraptor* or *Cryptovolans*) *pauli*

— 0.9 m (3 ft) TL, 0.95 m (3.1 ft) wingspan, 1.2 kg (2.5 lb)
FOSSIL REMAINS A few skulls and skeletons, extensive feathers.
ANATOMICAL CHARACTERISTICS Tail not very long. Trunk shallow because pubis double retroverted. Furcula and sternal plates large. Leg not very long.
AGE Early Cretaceous, early Aptian?
DISTRIBUTION AND FORMATION/S Northeastern China; upper? Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Placement in distinct genus problematic.

Jeholraptor haoiana

— 1.2 m (4 ft) TL, 3 kg (7 lb)
FOSSIL REMAINS Majority of skull and skeleton, immature.



Jeholraptor haoiana

Wulong bohaiensis juvenile

ANATOMICAL CHARACTERISTICS Head fairly robust and deep, jugal robust, and postorbital bar complete and broad, quadratojugal L shaped. Furcula and sternal plates not very large, hand not very slender. Two main toes fairly short, sickle claw not large, toe claws strongly curved.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Strongly curved toe claws indicate strong arboreality. Smaller furcula, sternum, and less gracile hand suggest was not as good a flier as *Sinornithosaurus*, hunted fairly large game.
NOTES Usual placement in earlier *S. millenii* incorrect because of very different quadratojugals and other reasons. L-shaped quadratojugals in this and *Wulong* suggest they are more closely related to one another than to other microraptorines and probably form their own subgroup.

Wulong bohaiensis

— Adult size uncertain
FOSSIL REMAINS Nearly complete skull and skeleton, extensive feathers, juvenile.
ANATOMICAL CHARACTERISTICS Jugal robust and postorbital bar complete, quadratojugal more L shaped. Hand not very slender.
AGE Early Cretaceous, early Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Details of back of skull obscure. Immature status hinders full analysis, large head is a juvenile feature.

Hesperonychus elizabethae

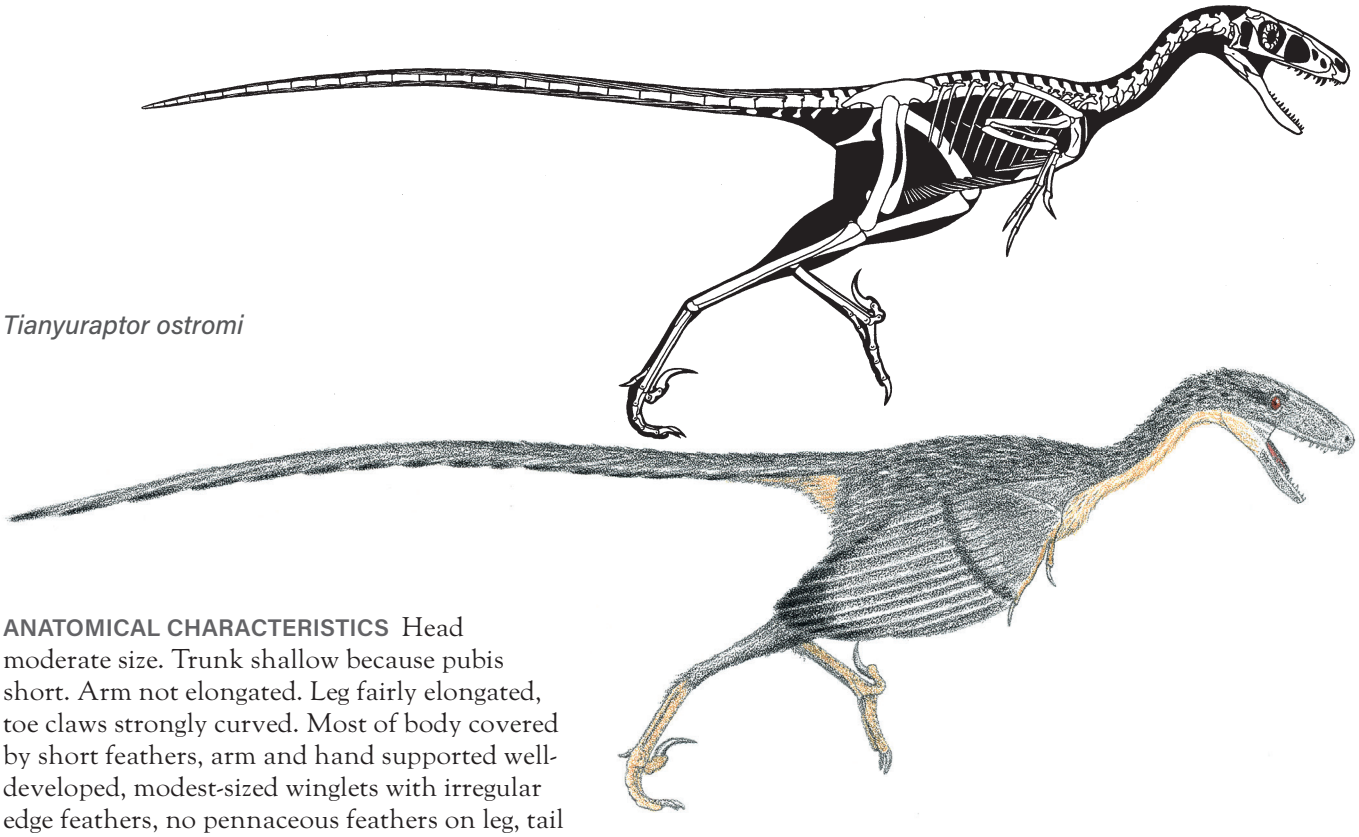
— 1 m (3 ft) TL, 1.5 kg (3.5 lb)
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Trunk shallow because pubis is double retroverted. Well-preserved hip socket directed more upward than in nonmicroraptor dinosaurs, indicating leg could be splayed more strongly sideways.
AGE Late Cretaceous, early late and middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; at least middle and upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES *Hesperonychus* implies that microraptorines or close relatives survived into the late Late Cretaceous.

— DROMAEOSAURID MISCELLANEA

NOTES The relationships of these dromaeosaurids are uncertain, as is that of fragmentary Early Cretaceous, North American *Yurgovuchia doellingi*.

Tianyuraptor ostromi

— 2 m (6.5 ft) TL, 11 kg (25 lb)
FOSSIL REMAINS Majority of skull and nearly complete skeleton, complete skull and majority of skeleton, extensive feathers.



Tianyuraptor ostromi

ANATOMICAL CHARACTERISTICS Head moderate size. Trunk shallow because pubis short. Arm not elongated. Leg fairly elongated, toe claws strongly curved. Most of body covered by short feathers, arm and hand supported well-developed, modest-sized winglets with irregular edge feathers, no pennaceous feathers on leg, tail supported a long set of feather vanes.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Substantial arboreal abilities. Modest-sized sickle claw indicates did not hunt particularly large prey. Winglets too small for significant flight, primary function probably display.
NOTES Probably includes *Zhenyuanlong suni*; if so, squared-off snout may be a male attribute, more pointed tip female. May be a close relative of microraptorines, possibly secondarily flightless.

Daurlong wangi

— 1.15 m (3.8 ft) TL, 5.5 kg (12 lb)
FOSSIL REMAINS Nearly complete skull and skeleton, some feathers, internal tissues.
ANATOMICAL CHARACTERISTICS Head robustly built, deep; snout square tipped, middle upper jaw teeth large. Tail short. Arm not elongated. Leg long partly because main toes long.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.

Daurlong wangi

DISTRIBUTION AND FORMATION/S Northern China; Longjiang.
HABITS Largely terrestrial predator, large teeth indicate hunted fairly large game.
NOTES Details of back portion of skull obscure. Only known short-tailed dromaeosaur.

Luanchuanraptor henanensis

— 1.1 m (3.5 ft) TL, 2 kg (4 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Central China; Qiupa.
NOTES May be an Asian unenlagiine.

— HALSZKARAPTORINES

SMALL DROMAEOSAURIDS LIMITED TO THE LATE CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Lightly built. Heads shallow, snouts somewhat duck-like, quadratojugal apparently not inverted T-shaped, teeth fairly numerous, small and unserrated. Necks fairly long and slender. Trunks shallow partly because ribs swept strongly back and out. Tails lack ossified rods. Arms short, outer fingers longest. Sickle claws modest sized.
HABITS Possibly partly aquatic, fishers, small game, insects.

Mahakala omnogovae

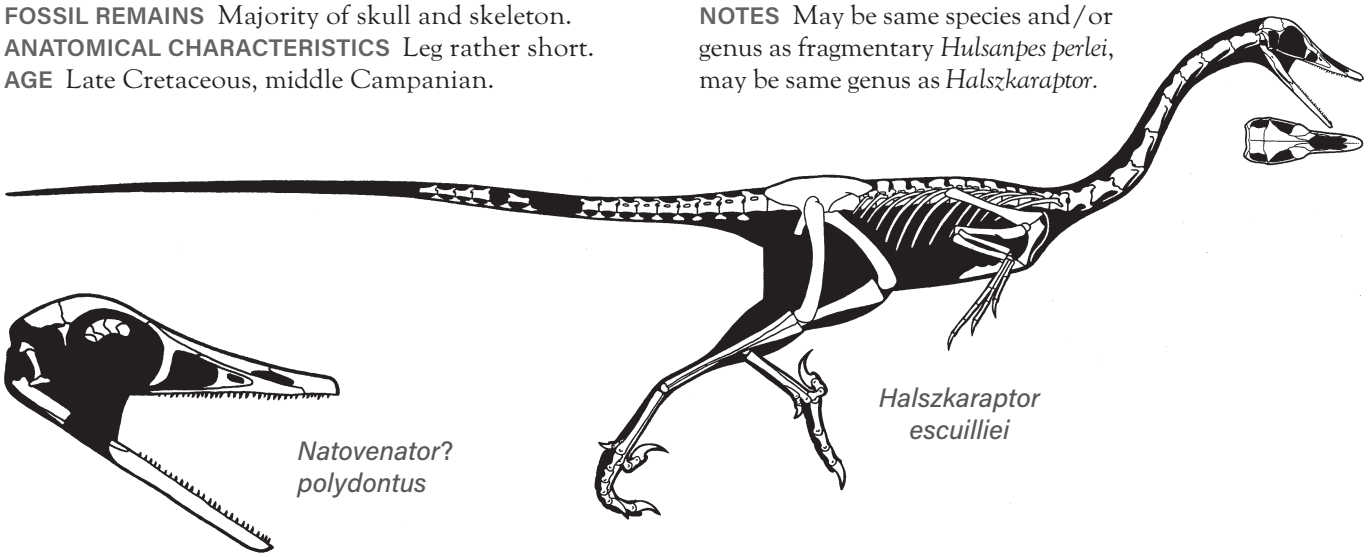
— 0.5 m (1.7 ft) TL, 0.1 (2 lb)
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Upper foot at least elongated.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Less aquatic than other group members.

Halszkaraptor escuilliei

— 0.9 m (3 ft) TL, 0.6 kg (1.4 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Leg rather short.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Djadokhta.
HABITAT/S Desert with dunes and oases.

Natovenator? polydontus

— 0.7 m (2.3 ft) TL, 0.3 kg (1.2 lb)
FOSSIL REMAINS Majority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.
NOTES May be same species and/or genus as fragmentary *Hulsanpes perlei*, may be same genus as *Halszkaraptor*.



— UNENLAGIINES

SMALL TO MEDIUM-SIZED FLYING AND FLIGHTLESS DROMAEOSAURIDS LIMITED TO THE LATE CRETACEOUS OF THE SOUTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Variable. Tails may lack ossified rods. Pubes vertical.
HABITS Appear to have been more prone to fishing.

NOTES Unenlagiines indicate that dromaeosaurids experienced a radiation of distinctive forms in the Southern Hemisphere that may have included fliers; losses and/or independent evolution of flight probably occurred.

Buitreraptor gonzalezorum

— 1.5 m (5 ft) TL, 3.6 kg (8 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head very long, shallow, and narrow, especially snout and lower jaw, teeth small, numerous, nonserrated. Arm and hand very elongated and very slender. Leg long and gracile, sickle claw fairly small.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
HABITS Hunted small game, probably fished using long snout and long arms and hands. Main defenses high speed and sickle claw.

Unenlagia comahuensis

— 3.5 m (12 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Sickle claw medium sized.
AGE Late Cretaceous, late Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.
HABITAT/S Well-watered woodlands with short dry season.
HABITS Probably able to dispatch fairly large prey. May have fished like other unenlagiines.
NOTES May include *U. paynemili* and *Neuquenraptor argentinus*.

Austroraptor cabazai

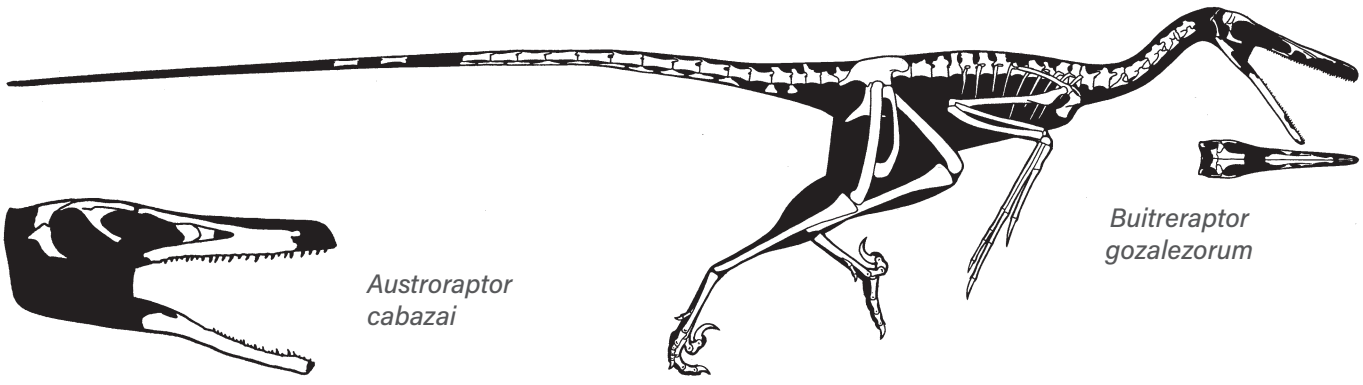
— 6 m (20 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head very long, shallow, especially snout and lower jaw, teeth fairly small, numerous, conical. Upper arm fairly short (rest unknown).
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Central Argentina; Allen.
HABITAT/S Semiarid coastline.
HABITS Probably fished, terrestrial prey also plausible.
NOTES Head form parallels that of spinosaurs.

Overoraptor chimentoi

— 3 m (10 ft) TL, 30 kg (60 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Arm not highly elongated.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
HABITS Nonflier.
NOTES Placement in unenlagiines not certain; not yet known whether the head was similar to the elongated form seen in larger unenlagiines.

Rahonavis ostromi

— 0.7 m (2.2 ft) TL, 1 kg (2 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Arm very large. Pubis vertical. Large sickle claw on hyperextendable toe. Quill nodes on trailing edge of upper arm indicate large flight feathers.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Madagascar; Maevarano.
HABITAT/S Seasonally dry floodplain with coastal swamps and marshes.
HABITS Diet may have included aquatic and/or terrestrial small prey, sickle claw possibly used to help dispatch larger prey. Capable of powered flight superior to that of *Archaeopteryx* and *Sapeornis*. Good climber and leaper. Defense included climbing and flight as well as sickle claws.
NOTES Placement in unenlagiines not certain; not yet known whether the head was similar to the elongated form seen in larger unenlagiines.



— DROMAEOSAURINES

SMALL TO LARGE DROMAEOSAURIDS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly variable. Strongly built. Front of snouts short. Teeth large, frontmost D-shaped in cross section.
HABITS Strong skulls and large, strong teeth indicate that dromaeosaurines used their heads to wound prey more than other dromaeosaurids.
NOTES Relationships within group uncertain, probably splittable into a number of subdivisions.

Utahraptor ostrommaysorum

— 6 m (20 ft) TL, 300 kg (600 lb)
FOSSIL REMAINS Numerous skeletal parts, juvenile to adult.
ANATOMICAL CHARACTERISTICS Very robustly built. Tail not highly elongated, flexible. Sickle toe claw large.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies and open woodlands, and riverine forests.
HABITS Not especially fast, an ambush predator that preyed on large dinosaurs.

Bambiraptor feinbergi

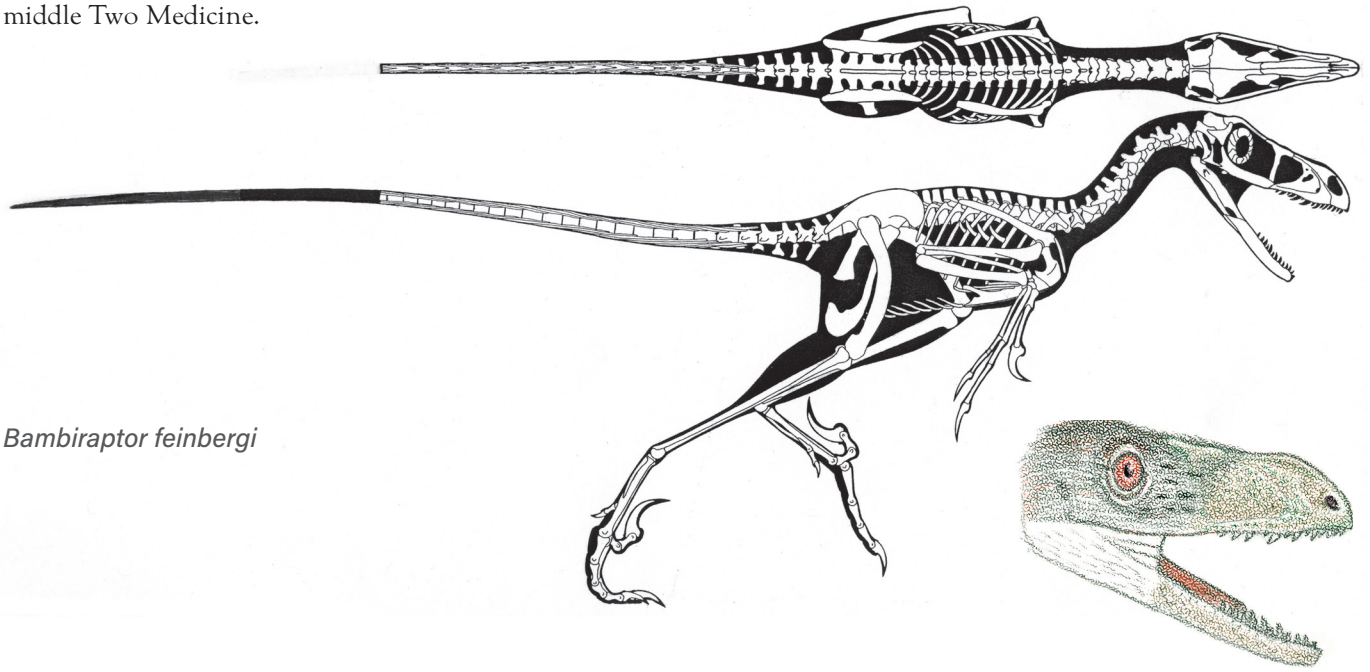
— 1.3 m (4 ft) TL, 7 kg (15 lb)
FOSSIL REMAINS Almost complete skull and skeleton, less complete skeleton.
ANATOMICAL CHARACTERISTICS Lightly built. Subrectangular head fairly deep. Arm and hand quite long. Pubis moderately retroverted, leg long, sickle claw large.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; middle Two Medicine.
HABITAT/S Seasonally dry upland woodlands.
HABITS Probably a generalist able to use head, arms, and sickle claw to handle and wound prey of various sizes, including small ornithopods and protoceratopsids. Long arms indicate good climbing ability and may be compatible with limited flight ability, especially in juveniles.

Achillobator giganticus

— 5 m (16 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head fairly deep. Pubis vertical, sickle claw large.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayanshiree.
HABITS Preyed on large dinosaurs.

Atrociraptor marshalli

— 2 m (6.5 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Partial skull and small portion of skeleton.
ANATOMICAL CHARACTERISTICS Head deep, teeth stout.



Bambiraptor feinbergi

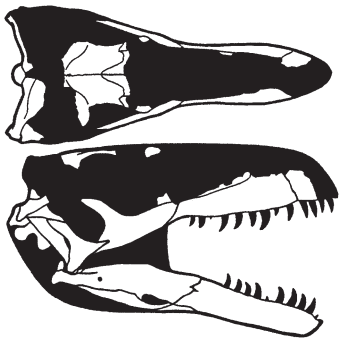
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta, Montana; lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Able to attack relatively large prey; used strong head and teeth to wound prey more than usual for dromaeosaurs.

Dromaeosaurus albertensis

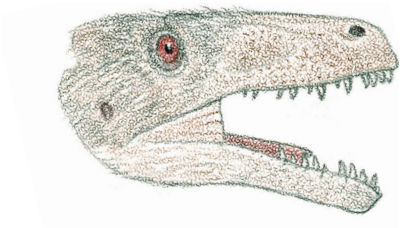
— 2 m (7 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Majority of skull, skeletal fragments.
ANATOMICAL CHARACTERISTICS Head broad and robust. Teeth large, stout, front tooth D-shaped in cross section.
AGE Late Cretaceous, late middle and/or early to middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; Dinosaur Park, level uncertain.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Able to attack relatively large prey.
NOTES Is not certain a large sickle claw belongs to this species. Not common in its habitat.

Adasaurus mongoliensis

— 2 m (7 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Head and body robustly built. Pubis moderately retroverted, sickle claw not large.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; middle or upper Nemegt.



Dromaeosaurus albertensis



HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
HABITS Able to attack relatively large prey. Did not use sickle claw as attack weapon as much as other similar-sized dromaeosaurids.

Dakotaraptor steini

— 6 m (20 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Lightly built. Leg long, sickle claw very large. Quill nodes on trailing edge of upper arm indicate large feather array.
AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S South Dakota; upper Hell Creek.
HABITAT/S Well-watered coastal woodlands, climate warmer than earlier in Maastrichtian.
HABITS Sickle a very powerful weapon.
NOTES May be a velociraptorine.

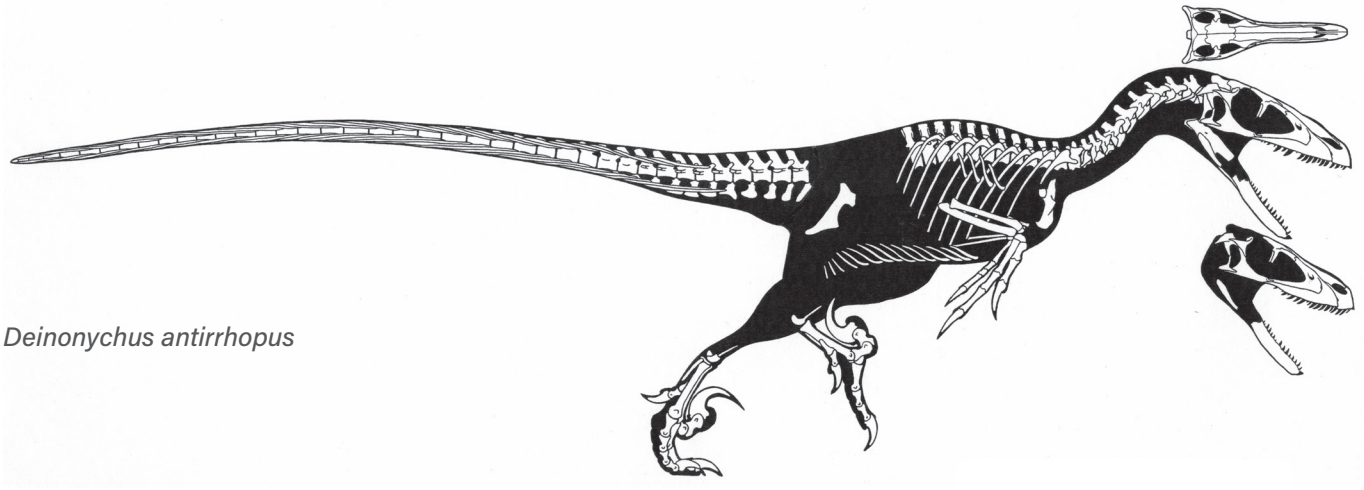
— VELOCIRAPTORINES

MEDIUM-SIZED DROMAEOSAURIDS LIMITED TO THE LATE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly strongly but not heavily built. Front of snouts markedly elongated. Teeth large, frontmost D-shaped in cross section. Sickle claws large.
HABITS Large sickle claws too big to be only for pinning prey, were primary weapons.
NOTES Very fragmentary, latest Cretaceous, North American *Acheroraptor temertyorum* probably belongs to this group.

Deinonychus antirrhopus

— 3.3 m (11 ft) TL, 65 kg (145 lb)
FOSSIL REMAINS Majority of several skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS Arm fairly long. Head lightly built, very large and long, subtriangular, snout arched in one fossil, may be depressed in another. Pubis moderately retroverted, leg moderately long, sickle claw large.
AGE Early Cretaceous, middle Albian.
DISTRIBUTION AND FORMATION/S Montana; upper Cloverly.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
HABITS Probably a generalist that ambushed and pursued small to big game. Juveniles relatively longer armed than adults and may have had limited flight ability.



Deinonychus antirrhopus

NOTES One of the classic dromaeosaurids, the primary basis of the *Jurassic Park* "raptors." Maxilla and snout not short and deep as often incorrectly restored. If snouts were arched in some individuals and depressed in others, may represent genders, or species. Remains from lower in Cloverly Formation usually placed in this species are probably one or more different taxa.

Velociraptor mongoliensis

— 2.5 m (8 ft) TL, 28 kg (60 lb)

FOSSIL REMAINS A number of complete and partial skulls and skeletons, juvenile to adult, completely known.

ANATOMICAL CHARACTERISTICS Head lightly built, long, snout extra long and shallow, strongly depressed in juveniles and less so in adults. Arm fairly long. Pubis

strongly retroverted. Sickle claw large. Quill nodes on trailing edge of upper arm indicate large feather array.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia, northern China; lower Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Probably a generalist that ambushed and pursued small to big game.
NOTES The other classic dromaeosaurid. Probably includes the contemporary *V. osmolskae*. Famous fighting pair preserves a *Velociraptor* and *Protoceratops* locked in comortal combat. May be direct ancestor of *V. mangas*.

Velociraptor (= *Tsaagan*) *mangas*
— 2 m (7 ft) TL, 21 kg (45 lb)
FOSSIL REMAINS Two? nearly complete skulls, one with majority of skeleton.
ANATOMICAL CHARACTERISTICS Head lightly built, snout not as shallow and depressed as that of *V.mongoliensis*.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia, northern China?; upper Djadokhta, upper Wulansuhai?
HABITAT/S Desert with dunes and oases.
HABITS Similar to *Velociraptor*.
NOTES Not different enough from *Velociraptor* to be different genus. May include *Linheraptor exquisitus*; if so, differing degrees of depression of snout may represent genders.

?Saurornitholestes langstoni
— Adult size uncertain
FOSSIL REMAINS Minority of skulls and skeletons, possibly juvenile.
ANATOMICAL CHARACTERISTICS Snout not shallow.

Velociraptor mongoliensis

Velocriraptor (= *Tsaagan*) *mangas*

AGE Late Cretaceous, late middle and early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta, possibly Montana; at least lower and middle Dinosaur Park, possibly upper Two Medicine.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and drier upland woodlands.
NOTES Based on questionably adequate remains, placement of Alberta and Montana remains in same taxon problematic.

— TROODONTS

SMALL TO MEDIUM-SIZED OMNIVOROUS DEINONYCHOSAURS FROM THE LATE JURASSIC UNTIL THE END OF THE DINOSAUR ERA OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly variable. Lightly built. Eyes face strongly forward, often very large; postorbital bars from robust to incomplete, teeth numerous, small, especially at front of upper jaw. Neck ribs usually so short they do not overlap, increasing flexibility of neck. Ossified sternal ribs and uncinates not present. Tails not as long as in dromaeosaurids. Ossified sternums absent. Arms not elongated. Pubes vertical or somewhat retroverted, legs long and gracile, sickle claws not greatly enlarged, but usually larger than other toe claws. Eggs moderately elongated, tapering.
HABITAT/S Highly variable, from deserts to polar forests.
HABITS Running performance very high, leaping and climbing ability poor compared to that of other deinonychosaurs. Pursuit predators that focused on smaller game and could fish, but could use sickle claws to dispatch larger prey, especially larger species with large claws, also used to pin down prey. Omnivorous in that also consumed significant plant material. Examples with very large eyes possibly more nocturnal than other dinosaurs. Eggs laid in pairs subvertically in rings, probably by more than one female in each nest, partly exposed so they could be brooded and incubated by adults sitting in center. Juveniles not highly developed so may have received care in or near nest.
NOTES Group name problematic because is based on teeth that are similar to those of pachycephalosaurs. Some researchers consider late Middle/early Late Jurassic *Anchiornis*, *Eosinopteryx*, and *Xiaotingia* of that age to be the earliest known members of this group. Incomplete postorbital bars and/or retroverted pubes in some examples may indicate close relationships to birds, or at least partly independent developments.

— BASO-TROODONTS

SMALL TROODONTS FROM THE LATE JURASSIC AND CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Highly uniform. Heads short, subrectangular.
NOTES May include above late Middle/early Late Jurassic potential troodonts.

Hesperornithoides miessleri

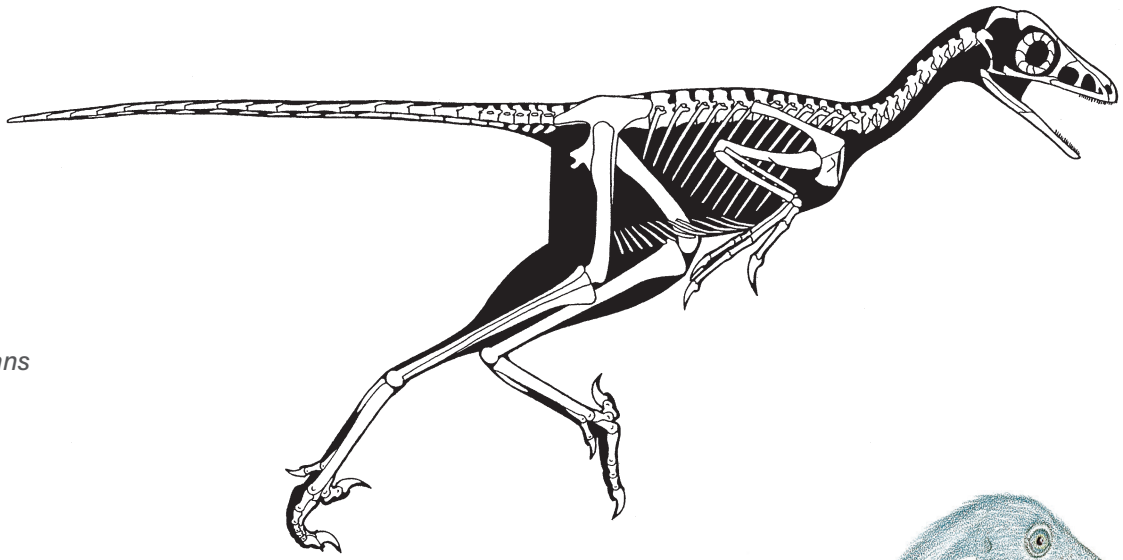
— 1 m (3 ft) TL, 3 kg (6 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Teeth and serrations fairly large.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Jinfengopteryx elegans

— 0.5 m (1.7 ft) TL, 0.5 kg (1 lb)
FOSSIL REMAINS Complete skull and skeleton, feathers.
ANATOMICAL CHARACTERISTICS Head lightly built, postorbital bar incomplete. Arms fairly large. Pubis vertical. Well-developed pennaceous feathers line entire tail.
AGE Late Late Jurassic or early Early Cretaceous.
DISTRIBUTION AND FORMATION/S Northeastern China; Qiaotou.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.
HABITS Diet mainly small game and insects. Roundish objects in belly region may be large seeds or nuts.
NOTES May be a juvenile. Originally thought to be a bird close to *Archaeopteryx*; is the earliest certain troodontid known from skeletal remains.

Liaoningvenator curriei

— 0.9 m (2.9 ft) TL, 1.8 kg (4 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head lightly built. Pubis retroverted, leg very long partly because main toes long.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Diet mainly small game and insects.



Jinfengopteryx elegans

Liaoningvenator curriei

Mei long

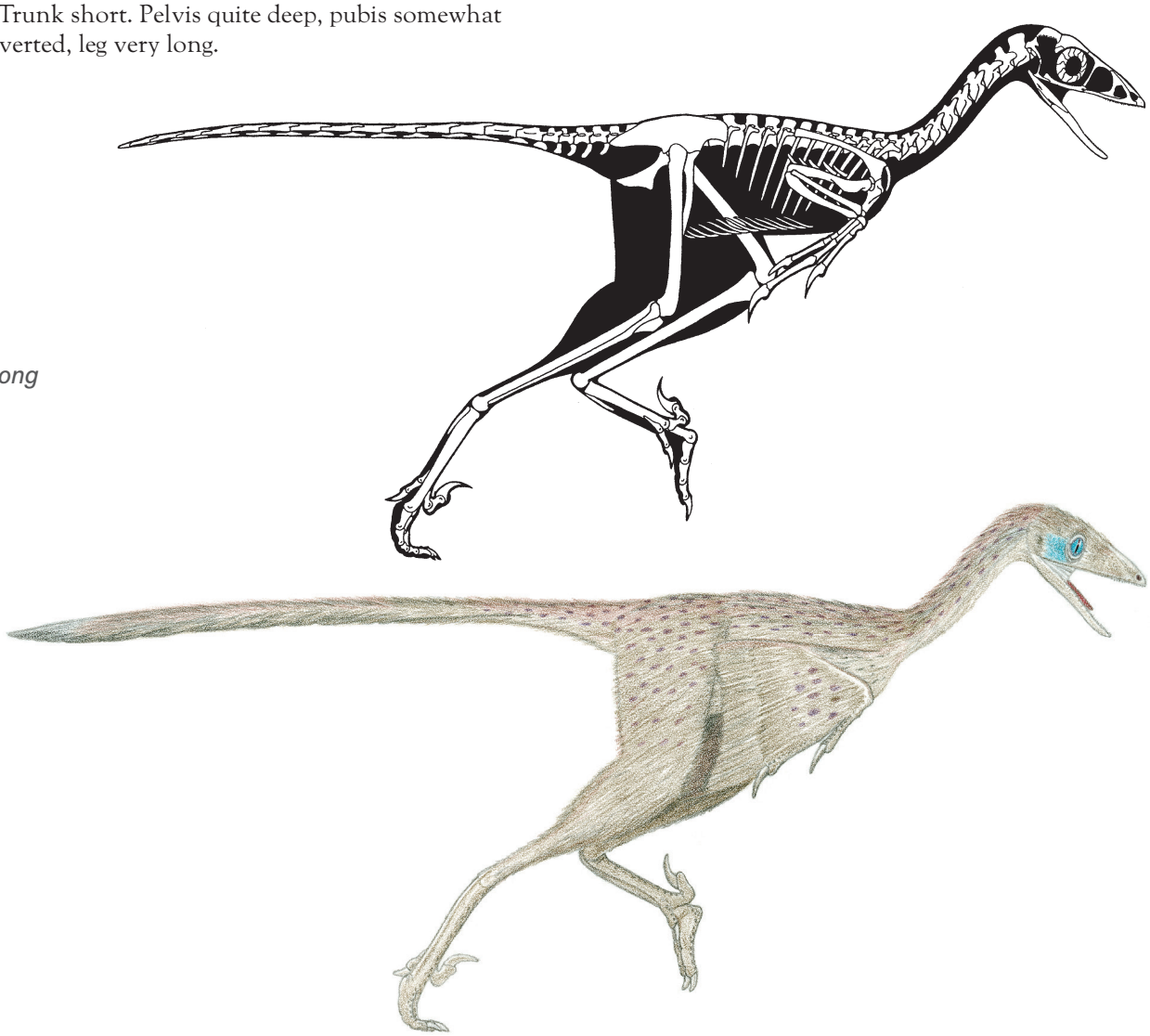
— 0.45 m (1.4 ft) TL, 0.5 kg (1 lb)
FOSSIL REMAINS Several nearly complete skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head lightly built, postorbital bar incomplete, teeth small, unserrated. Arm fairly large. Pubis slightly retroverted.
AGE Early Cretaceous, at least earliest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Diet mainly small game and insects.

Sinovenator changii

— 2 m (6.5 ft) TL, 27 kg (60 lb)
FOSSIL REMAINS Numerous skulls and skeletons, complete to partial skull, adult and juvenile.
ANATOMICAL CHARACTERISTICS Lightly built. Postorbital bar complete, teeth fairly small, serrations absent in front teeth, small and limited to back edge on rest. Trunk short. Pelvis quite deep, pubis somewhat retroverted, leg very long.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

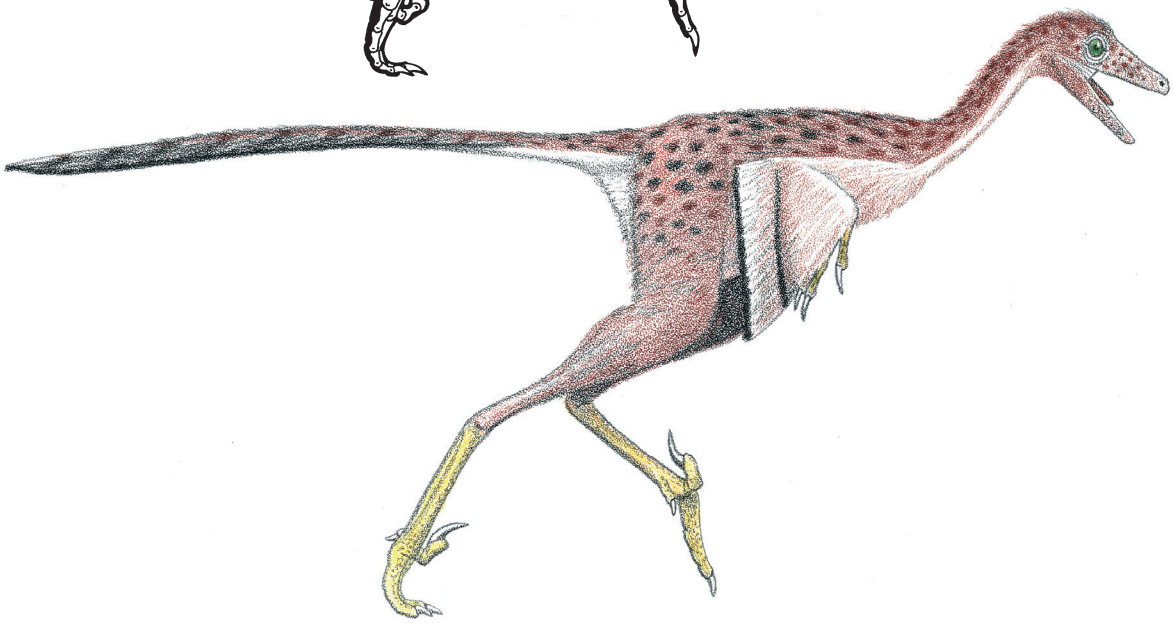
Jianianhualong tengi

— Adult size not certain
FOSSIL REMAINS Majority of skull and skeleton, possibly juvenile.
ANATOMICAL CHARACTERISTICS Postorbital bar complete, teeth fairly small, serrations absent on front teeth, small and limited to back edge on rest. Tail fairly long. Pelvis not deep, pubis somewhat retroverted, leg rather short.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.



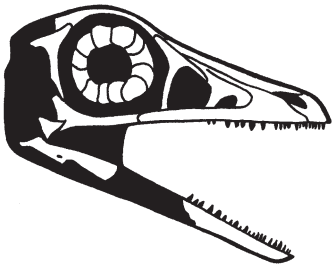
Mei long

Sinovenator changii



Jianianhualong tengi

Daliansaurus liaoningensis
— 0.7 m (2.5 ft) TL, 1.5 kg (3 lb)
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Teeth fairly large, serrations absent in front teeth, small and limited to back edge on rest. Outer toe claw as large as second.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.



Almas ukhaa

HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS That not just hyperextendable second toe was large indicates different hunting and other habits from small basal troodonts.

Almas ukhaa
— Adult size uncertain
FOSSIL REMAINS Majority of two skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS. TEETH SMALL. PUBIS RETROVERTED.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta, Wulansuhai?
NOTES From the same age Wulansuhai Formation, *Papiliovenator neimengguensis* may be more mature member of this species, or at least genus.

— TROODONT MISCELLANEA

NOTES Troodonts that are neither baso-troodontines nor troodontines, relationships uncertain.

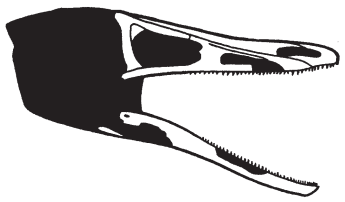
Sinornithoides youngi
— 1.1 m (3.5 ft) TL, 2.9 kg (5.5 lb)
FOSSIL REMAINS Partial skull and complete skeleton, not fully mature.
ANATOMICAL CHARACTERISTICS Head long and shallow, teeth and denticles small. Arm fairly small. Pubis vertical.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Northern China; Ejinhoro.
NOTES Skeleton found curled in sleeping position similar to *Mei*.

Sinusonasus magnodens
— 1 m (3.3 ft) TL, 2.5 kg (5.5 lb)
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head long and shallow, serrations absent in front teeth, small and limited to back edge on rest, teeth relatively large.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Attacked bigger game than *Sinovenator*, smaller game than *Sinornithosaurus*.

Sinornithoides youngi

Xixiasaurus henanensis
— 1.5 (5 ft) TL, 8 kg (18 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head fairly shallow, teeth fairly large, sharp, unserrated.
AGE Late Cretaceous, probably Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Majiacun.

Byronosaurus jaffei
— 1.5 m (5 ft) TL, 8 kg (20 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Snout very long and very shallow, a little depressed, eyes not especially large, teeth sharp, unserrated.



Byronosaurus jaffei

AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Hunted small game, possibly fished, probably less nocturnal than most troodonts.
NOTES *Almas ukhaa* may be juvenile of this species.

— TROODONTINES

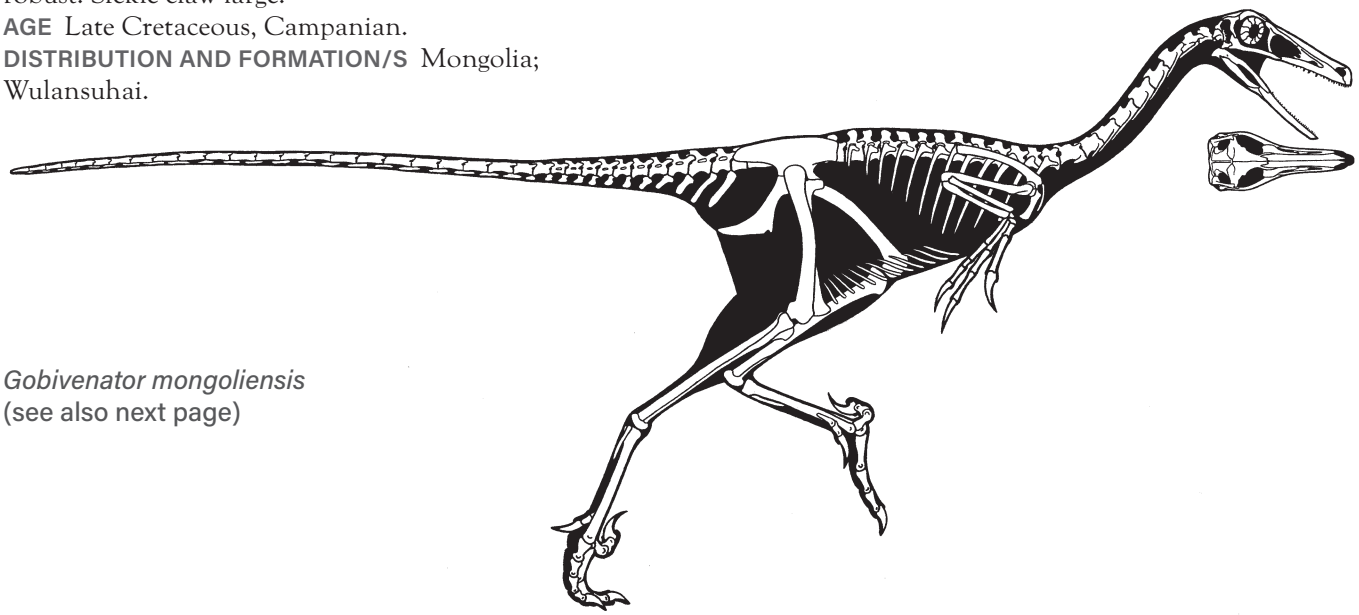
MEDIUM-SIZED TROODONTS LIMITED TO THE LATE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Uniform. Heads long and shallow, postorbital bars robust. Legs long.
NOTES May include above late Middle/early Late Jurassic potential troodonts.

Talos sampsoni
— 2 m (7.5 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Leg very slender.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Utah; middle Kaiparowits.

Linhevenator tani
— 2.1 m (7 ft) TL, 20 kg (40 lb)
FOSSIL REMAINS Poorly preserved partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Arm short and robust. Sickle claw large.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; Wulansuhai.
HABITS Strong arm and large sickle-claw foot weapon indicate hunted bigger game than other troodonts.

Gobivenator mongoliensis
— 1.7 m (5.5 ft) TL, 10 kg (22 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Snout semitubular, teeth small and unserrated. Arm fairly small. Pubis vertical.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.
HABITAT/S Desert with dunes and oases.



Gobivenator mongoliensis
(see also next page)

Gobivenator mongoliensis

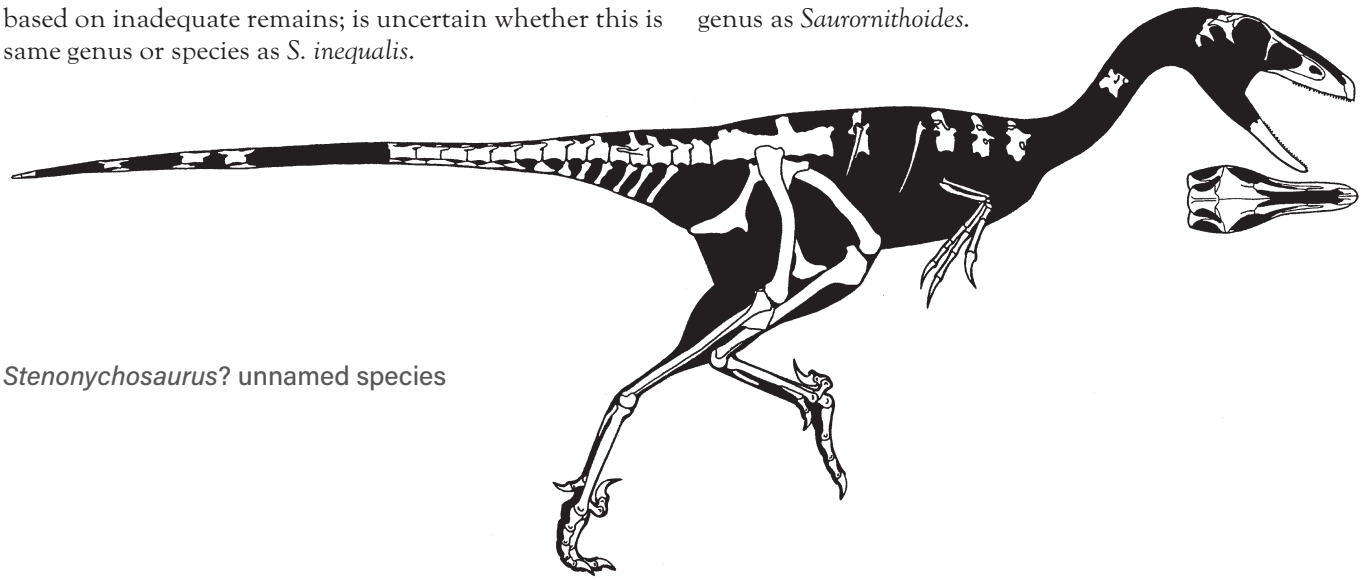
HABITS Hunted both small and large game, possibly fished. Possibly more nocturnal than most theropods.
NOTES The first nearly completely known troodont.

Stenonychosaurus? unnamed species

— 3.2 m (10 ft) TL, 75 kg (165 lb)
FOSSIL REMAINS Skull and skeletal parts. Complete nests.
ANATOMICAL CHARACTERISTICS Head fairly robustly built, shallow, snout semitubular, teeth with large denticles. Pubis vertical. Elongated eggs 18 cm (7 in) long.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.
HABITAT/S Seasonally dry upland woodlands.
HABITS Hunted both small and large game, possibly fished.
NOTES Usually placed in *Troodon formosus*, which is based on inadequate remains; is uncertain whether this is same genus or species as *S. inequalis*.

Stenonychosaurus? *inequalis*?

— 2.5 m (8 ft) TL, 35 kg (70 lb)
FOSSIL REMAINS Minorities of a few skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head fairly robustly built, shallow, snout semitubular, teeth with large denticles.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Hunted both small and large game, possibly fished.
NOTES Based on questionably adequate remains, lack of information on its pubis hinders determining whether is close to either *Latenivenatrix*, or to *Stenonychosaurus* unnamed species; may be same genus as *Saurornithoides*.

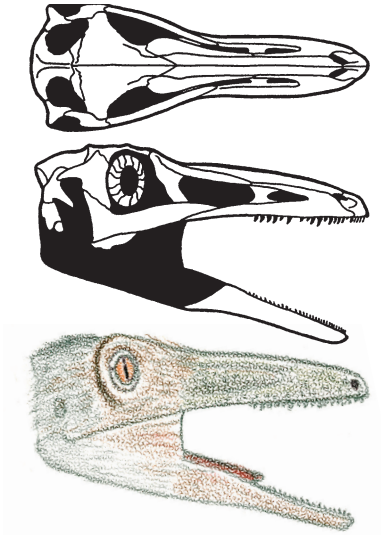


Stenonychosaurus? unnamed species

Stenonychosaurus? *inequalis*?

Latenivenatrix mcmasterae

— 5 m (16 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minorities of a few skulls and skeletons.
ANATOMICAL CHARACTERISTICS Pubis somewhat retroverted.
AGE Late Cretaceous, middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Hunted larger game than smaller troodonts.
NOTES Probably not same genus as earlier, different *Stenonychosaurus inequalis*. Largest known troodont.



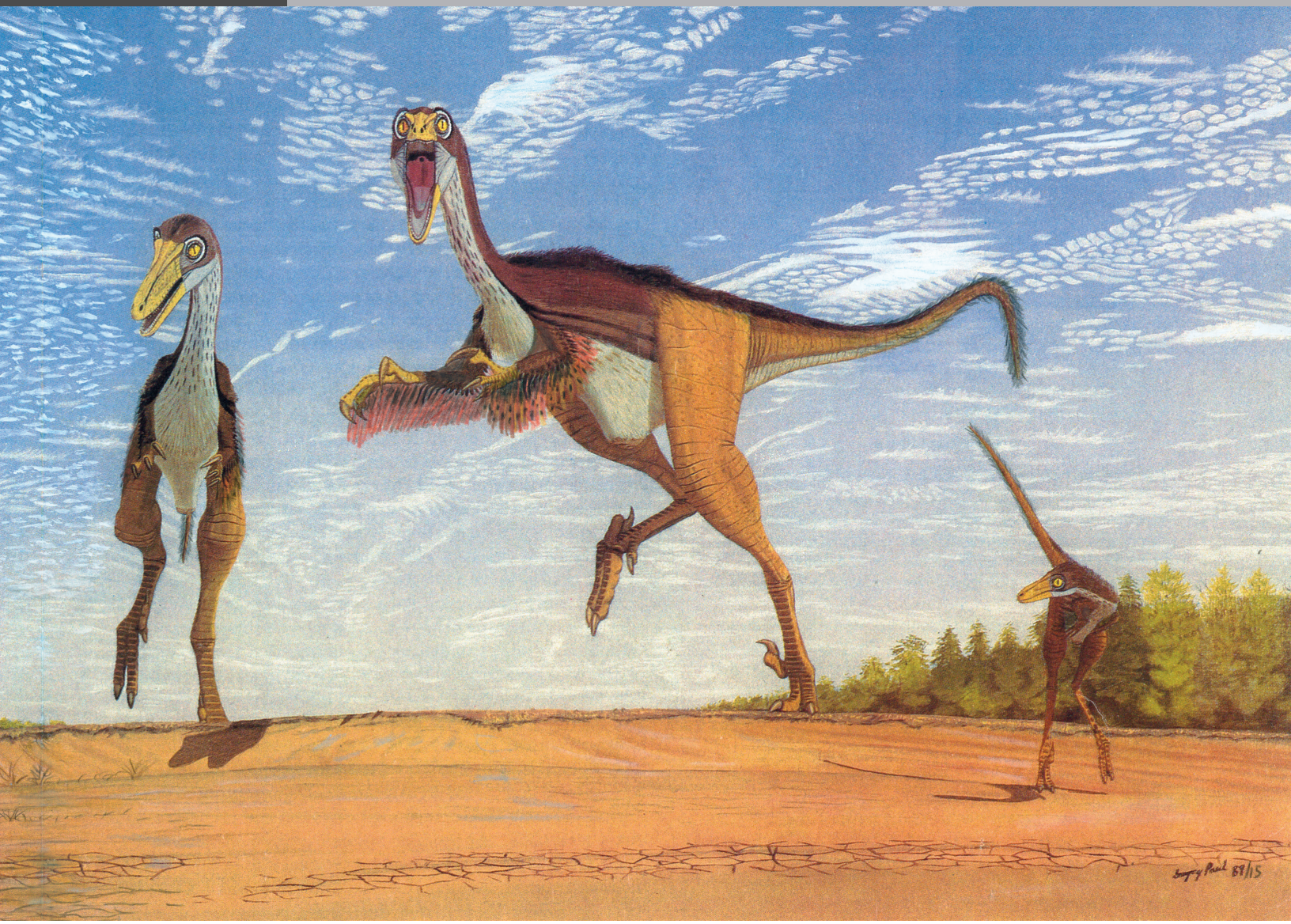
Saurornithoides (or *Zanabazar*) *junior*

Saurornithoides mongoliensis

— Adult size uncertain
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head fairly robustly built, shallow, snout semitubular, teeth with large denticles. Pubis vertical.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Similar to *Stenonychosaurus*.
NOTES May have been smaller than *S. junior*. *Saurornithoides* may be same genus as *Stenonychosaurus*. May be an ancestor of *S. junior*.

Saurornithoides (or *Zanabazar*) *junior*

— 2.3 m (7.5 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Majority of a skull and minority of the skeleton.
ANATOMICAL CHARACTERISTICS Head fairly robustly built, shallow, snout semitubular, teeth with large denticles.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; middle or upper Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
HABITS Similar to *S. mongoliensis*.
NOTES Available evidence insufficient to make separate genus from *Saurornithoides*.



Saurornithoides

— THERIZINOSAURIFORMS

SMALL TO GIGANTIC FLYING AND FLIGHTLESS HERBIVOROUS AVEAIRFOILANS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Variable. Heads somewhat elongated, blunt upper beak, extra joint in lower jaw absent, teeth small, blunt, leaf shaped, not serrated. Neck ribs usually so short they do not overlap, increasing flexibility of neck. Tails from very long to very short. Arms long, semilunate carpal from well to poorly developed. Feet not narrow, three to four load-bearing toes. Gastroliths often present.
HABITS Herbivores.
NOTES Jeholornids, therizinosaurians, and avians and their common ancestor, operative only if three groups form a clade that excludes all other dinosaurs except oviraptorosaurs.

— JEHOLORNIDS

SMALL FLYING AVEAIRFOILANS OF THE EARLY CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Beaks well developed, two stout upper teeth, lower teeth restricted to front. Tails long and slender. Furculas and sternal plates large, arms longer and much more strongly built than legs, outer upper hand bones curved, outer and central fingers stiffened and bases flattened to better support fully developed, long wings

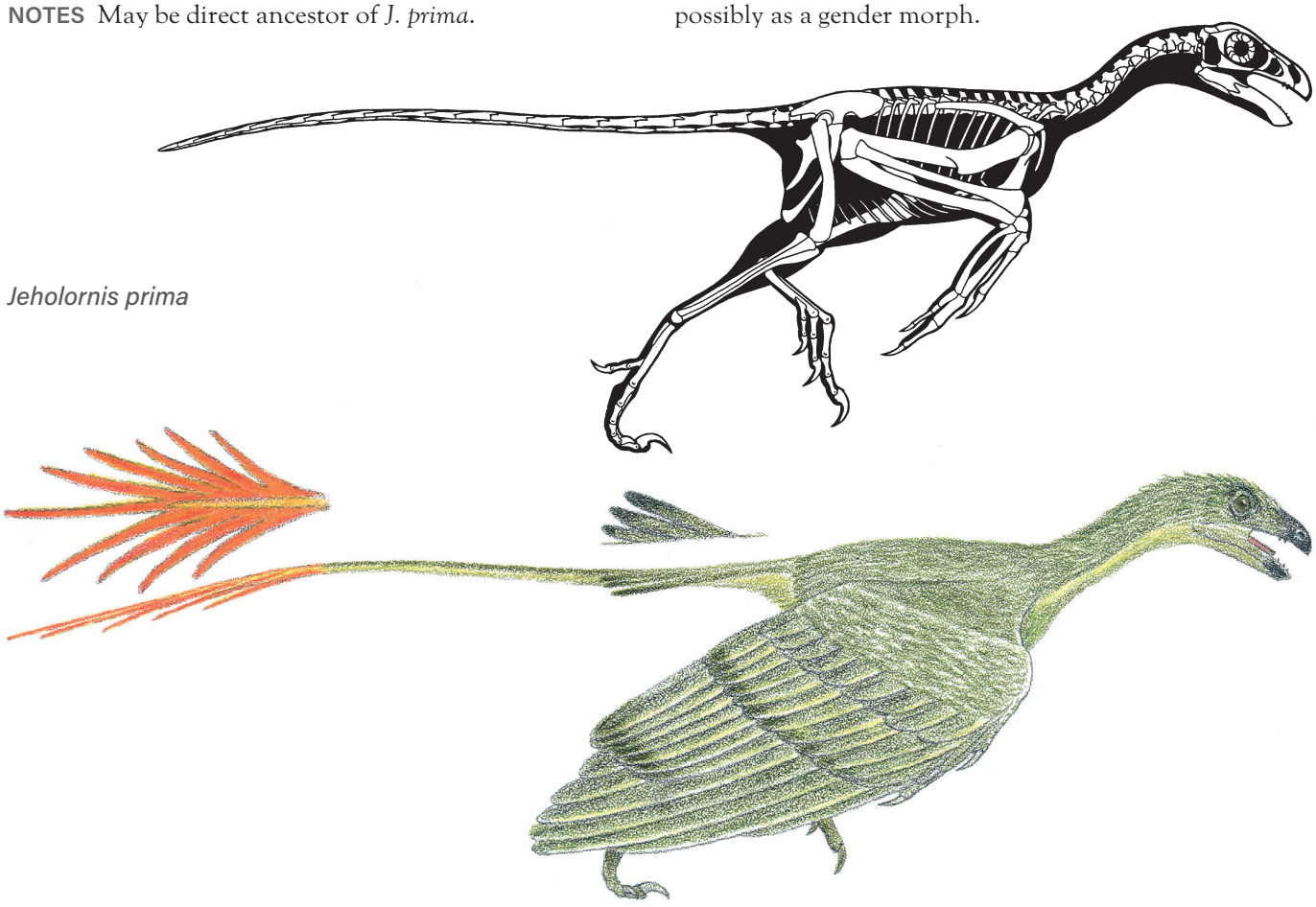
made of asymmetrical feathers. Pubes moderately retroverted. Most of body covered by short feathers, base of tails supported feather fan, tails ended with palmlike feather frond, at least in some cases.
HABITS Powered flight fairly well developed. Feather fan at tail base aerodynamic, feather frond at tail tip predominantly for display. Seeds and leaves found in guts of some fossils.
NOTES A very therizinosaur-like skull strongly suggests a close relationship. Although not the direct ancestors of therizinosauroids, jeholornids may represent the long-headed, long-tailed, flying basal birds that therizinosaurs evolved from.

Jeholornis curvipes

— 0.7 m (2.5 ft) TL, 0.8 kg (1.8 lb)
FOSSIL REMAINS Complete but poorly preserved skulls with skeletons.
ANATOMICAL CHARACTERISTICS As for group.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES May be direct ancestor of *J. prima*.

Jeholornis prima

— 0.7 m (2.5 ft) TL, 0.8 kg (1.8 lb)
FOSSIL REMAINS Skulls and skeletons, extensive feathers.
ANATOMICAL CHARACTERISTICS As for group.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Probably includes *J. palmapenis*, possibly as a gender morph.



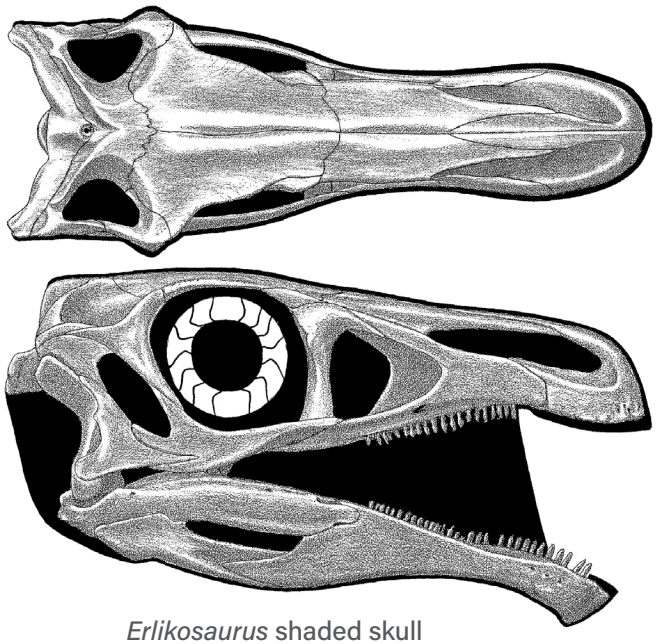
Jeholornis prima

— THERIZINOSAURIANS

SMALL TO GIGANTIC HERBIVOROUS FLIGHTLESS AVEAIRFOILANS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Variable. Heads small, cheeks very probably present, jaw gap limited. Necks long and slender. Trunks tilted upward from retroverted and therefore horizontal pelves and tails, bellies large. Tails from very long to very short. Furculas and sternals not large, arms long but shorter and weaker than legs, half-moon carpal

blocks from well to poorly developed, finger claws large. Feet not narrow, three to four load-bearing toes, toe claws enlarged. Feathers simple.
HABITS Predominantly browsing herbivores, picked up small animals on occasion. Too slow to readily escape predatory theropods, main defense long arms and hand claws as well as kicks from clawed feet.
ENERGETICS Energy levels and food consumption probably low for dinosaurs.
NOTES The most herbivorous of the theropods, therizinosaurs are so unusual in their form that before sufficient remains were found it was uncertain they were avepods, relationships to prosauropods once being an alternative. The redevelopment of a complete inner toe within the group is an especially unusual evolutionary reversal, partly paralleled in *Chilesaurus* and *Balaur*. Relationships within avepods remain uncertain. May not be aveairfoilans, may not have descended from fliers, may have descended from very early fliers near base of aveairfoilans. If are secondarily flightless aveairfoilans, may have descended from long-skulled herbivorous early birds more than once, from fliers long tailed and then short tailed. Or tail reduction occurred independently in therizinosaurs if they never had flying ancestors as per conventional theory. The modest extent of initial reversals from therizinosaur-like fliers like jeholornids to the first flightless therizinosaurs, the presence of a number of flight-related features in early therizinosaurs, and their progressive reduction as the group evolved toward massive ground herbivores are strongly compatible with an origin among fliers. Lack of pennaceous feathers is paralleled in birds with long history of flightlessness such as ratites.



Erlikosaurus shaded skull

— BASO-THERIZINOSAURIANS

MEDIUM-SIZED THERIZINOSAURIANS LIMITED TO THE EARLY CRETACEOUS.

ANATOMICAL CHARACTERISTICS Trunks only modestly tilted up, gastralia flexible. Lunate carpals well developed, finger claws hooked. Front of pelves not strongly flared out sideways, legs fairly long, hind feet still tridactyl with inner toes still a short hallux, claws not greatly enlarged.
HABITS Better runners than more advanced therizinosaurs.

Fukuivenator paradoxus

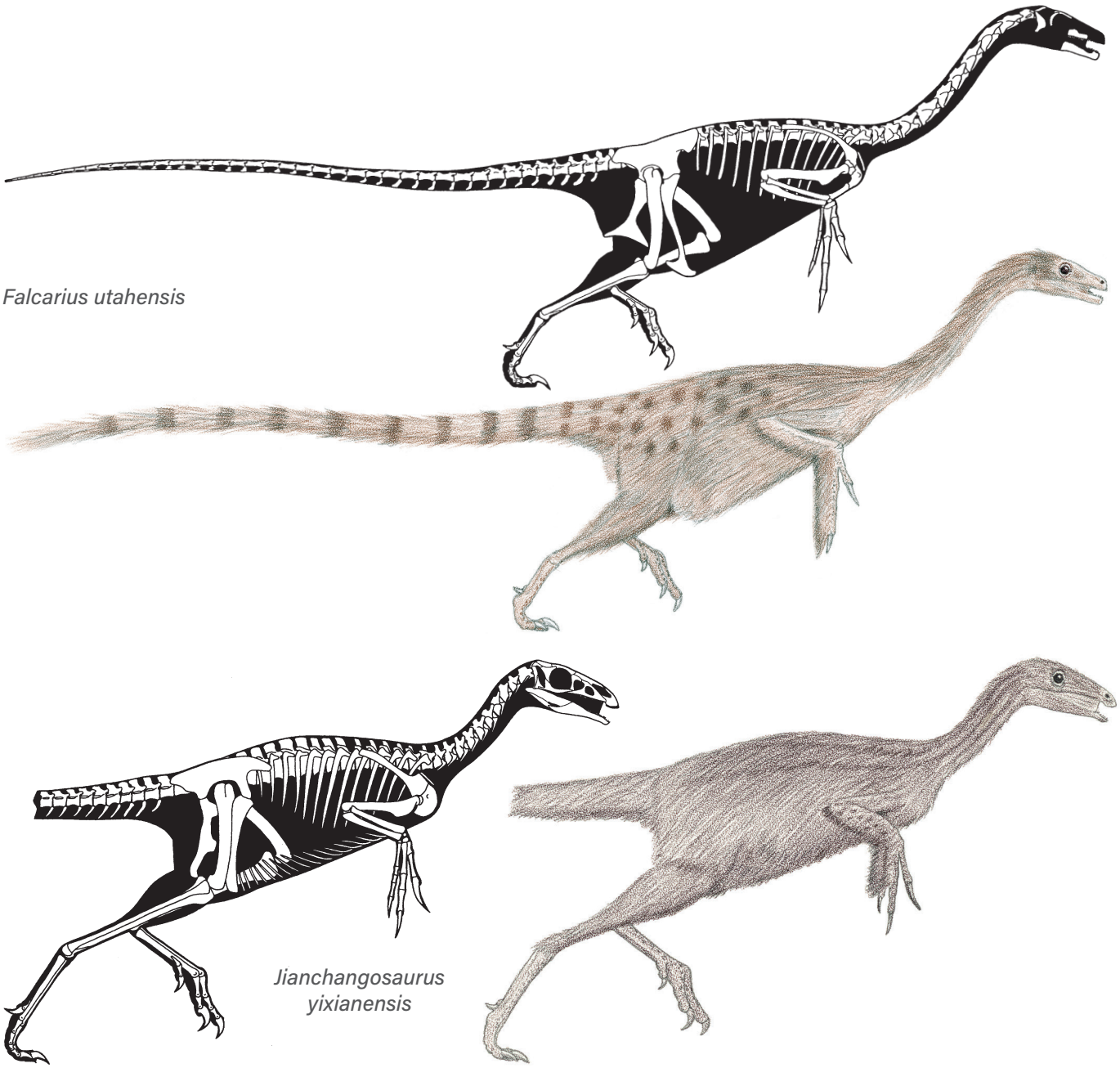
— 2 m (6.5 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Teeth sharp, some large, recurved. Tail long. Shoulder girdle not birdlike. Orientation of pubis uncertain.
AGE Early Cretaceous, Barremian or Aptian.
DISTRIBUTION AND FORMATION/S Central Japan; Kitadani.

Falcarius utahensis

— 4 m (13 ft) TL, 120 kg (250 lb)
FOSSIL REMAINS Minority of skull and almost complete skeletal remains known from dozens of partial fossils, juvenile to adult.
ANATOMICAL CHARACTERISTICS Tail very long. Shoulder girdle birdlike. Pubis orientation possibly vertical.
AGE Early Cretaceous, late Berriasian.
DISTRIBUTION AND FORMATION/S Utah; lowermost Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
NOTES Lack of pelvis from a single individual leaves orientation of pubis problematic.

Jianchangosaurus yixianensis

— Total length uncertain, 26 kg (60 lb)
FOSSIL REMAINS Complete skull and majority of skeleton, some feathers.
ANATOMICAL CHARACTERISTICS Tip of lower jaw downturned. Tail not abbreviated but length uncertain. Shoulder girdle not birdlike. Pubis moderately retroverted. Leg long.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian, level uncertain.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Best runner among therizinosaurs.



— THERIZINOSAUROIDS

SMALL TO LARGE THERIZINOSAURIANS OF THE CRETACEOUS.

ANATOMICAL CHARACTERISTICS Fairly variable. Tip of lower jaws downturned. Skeletons robustly built. Tails short. Shoulder girdles not birdlike, arms moderately long, lunate carpal blocks less well developed, fingers not very long, finger claws large hooks. Front of pelves enlarged and flared sideways, and pubes retroverted to support bigger bellies, feet short and broad with four complete toes, toe claws not very enlarged. Known eggs subspherical.
HABITS Buried nests and lack of evidence of brooding indicate little or no parental care. Well-developed hatchlings probably able to leave nest immediately on hatching.

Beipiaosaurus inexpectus

— 1.8 m (6 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Skull, two partial skeletons, feathers.
ANATOMICAL CHARACTERISTICS Head shallow, sharply tapering toward front. Vertebrae at tip of tail fused into a small pygostyle. Arrays of long, tapering, band-like feathers atop and beneath back of head; simple feathers on much of body.

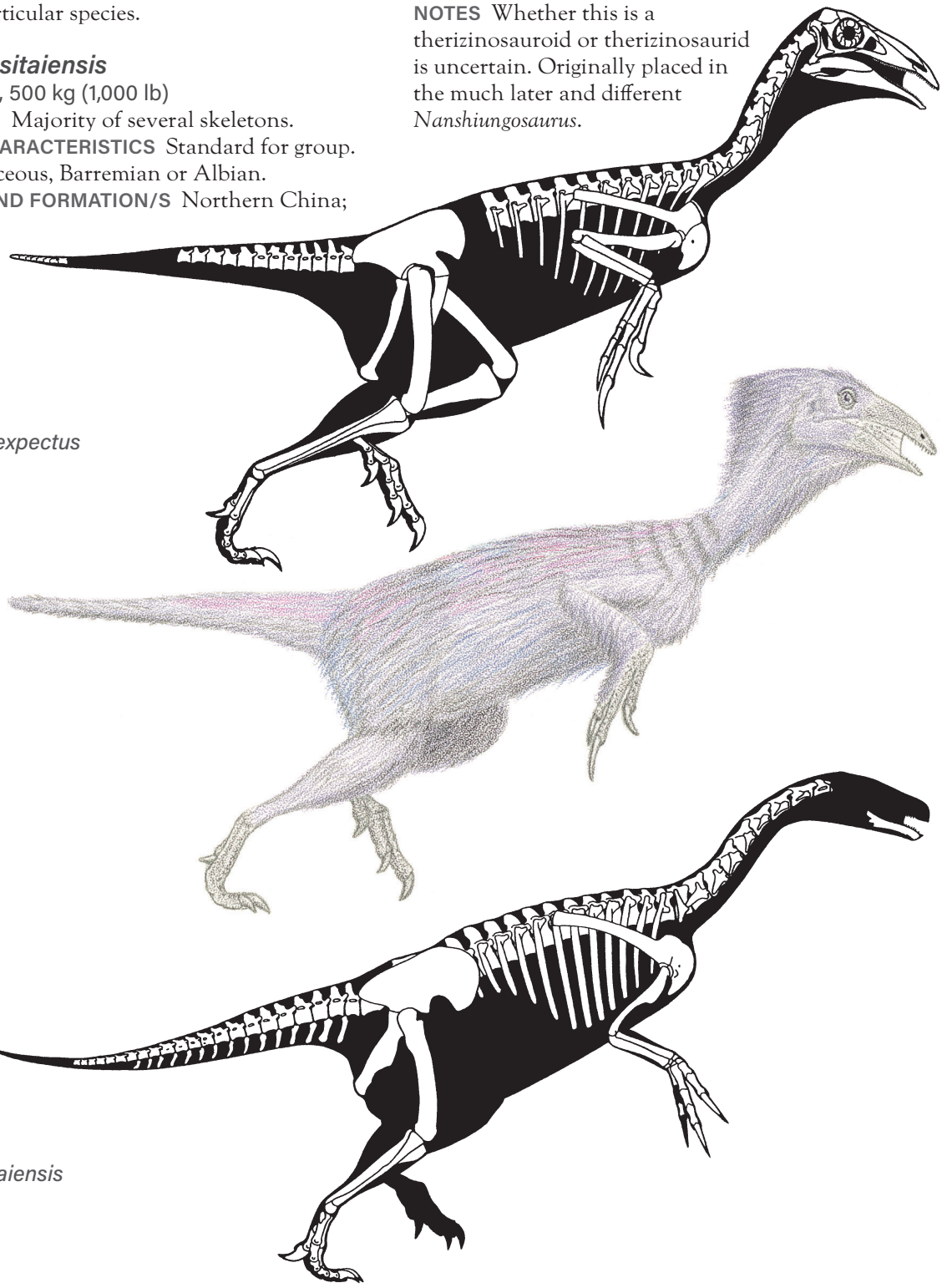
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Feather arrays for display.
NOTES Is not certain that skull and front half of skeleton belong to this particular species.

Alxasaurus elesitaiensis

— 4 m (13 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Majority of several skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Cretaceous, Barremian or Albian.
DISTRIBUTION AND FORMATION/S Northern China; Bayingobi.

Unnamed genus *bohlini*

— 6 m (20 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Northern China; Xinminbao Group.
NOTES Whether this is a therizinosauroid or therizinosaurid is uncertain. Originally placed in the much later and different *Nanshiungosaurus*.



Beipiaosaurus inexpectus

Alxasaurus elesitaiensis

Suzhousaurus megatheroides
— 6 m (20 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Northern China; Xinminbao Group.
NOTES Whether this is a therizinosauroid or therizinosaurid is uncertain.

— THERIZINOSAURIDS

MEDIUM-SIZED TO GIGANTIC THERIZINOSAUROIDS OF THE LATE CRETACEOUS.

ANATOMICAL CHARACTERISTICS Uniform. Tip of lower jaws downturned. Skeletons more robustly built. Trunks more strongly tilted up. Tails short. Shoulder girdles not birdlike, semilunate carpal blocks more poorly developed so wrist flexion reduced, fingers not very long but bearing very large claws. Front of pelves further enlarged and flared sideways to support bigger bellies, feet broad with four toes, toe claws large.
HABITS Strong upward tilt of trunk indicates these were high-level browsers.
NOTES The dinosaur group most similar to the recent giant ground sloths.

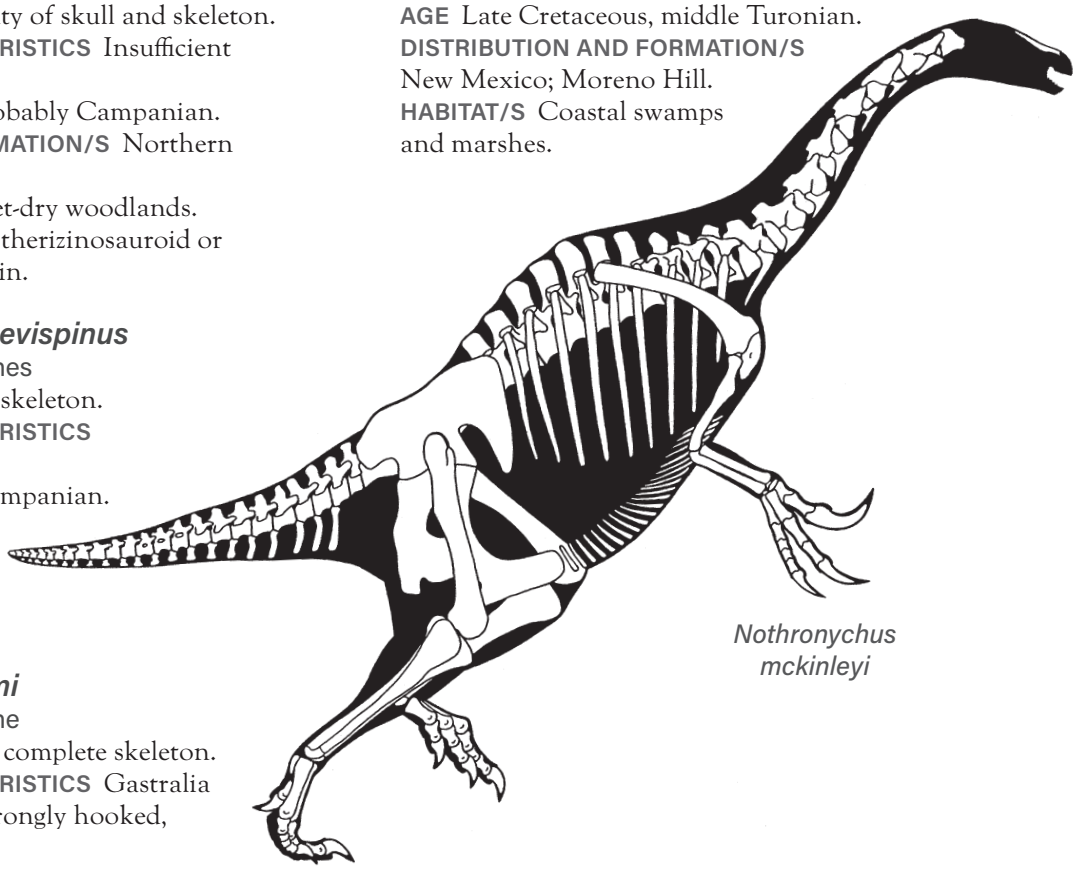
Erliansaurus bellamanus
— 4 m (13 ft) TL, 1 tonne
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Northern China; Iren Dabasu.
HABITAT/S Seasonally wet-dry woodlands.
NOTES Whether this is a therizinosauroid or therizinosaurid is uncertain.

Neimongosaurus yangi
— 3 m (10 ft) TL, 350 kg (800 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably Campanian.
DISTRIBUTION AND FORMATION/S Northern China; Iren Dabasu.
HABITAT/S Seasonally wet-dry woodlands.
NOTES Whether this is a therizinosauroid or therizinosaurid is uncertain.

Nanshiungosaurus brevispinus
— 5 m (16 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Northern China; Yuanpu.

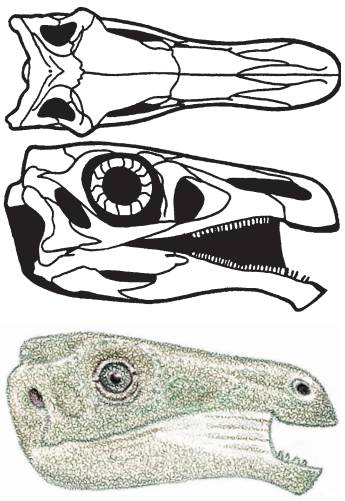
Nothronychus graffami
— 4.2 m (14 ft) TL, 1 tonne
FOSSIL REMAINS Nearly complete skeleton.
ANATOMICAL CHARACTERISTICS Gastralia inflexible. Finger claws strongly hooked, toe claws not enlarged.
AGE Late Cretaceous, early Turonian.
DISTRIBUTION AND FORMATION/S Utah; Tropic Shale.
HABITAT/S Coastal swamps and marshes.
NOTES Found as drift in nearshore marine sediments. Inflexibility of gastralia caused by lack of major changes in volume of belly in a nongorging, constantly feeding herbivore. May be direct ancestor of *N. mckinleyi*.

Nothronychus mckinleyi
— 5 m (17 ft) TL, 1.7 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Same as for *N. graffami*.
AGE Late Cretaceous, middle Turonian.
DISTRIBUTION AND FORMATION/S New Mexico; Moreno Hill.
HABITAT/S Coastal swamps and marshes.



Nothronychus mckinleyi

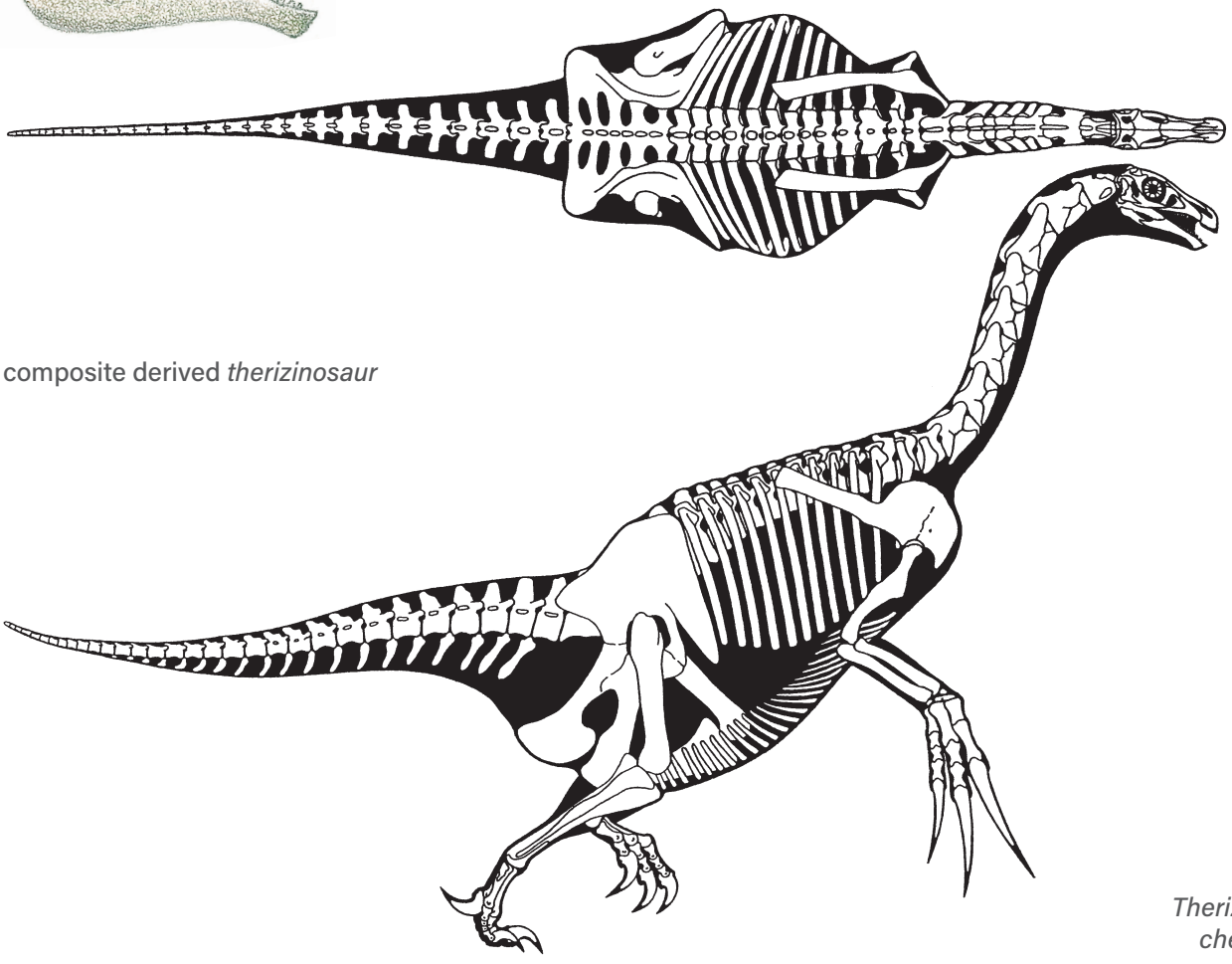
Segnosaurus galbinensis
— 6 m (20 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Cheeks not as extensive as those of *Erlikosaurus*. Front of pelvis greatly enlarged, toe claws enlarged.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayenshiree Svita.
HABITS Used large clawed feet for defense as well as hands.
NOTES *Enigmosaurus mongoliensis* may be the same as this species or *Erlikosaurus*.



Erlikosaurus andrewsi

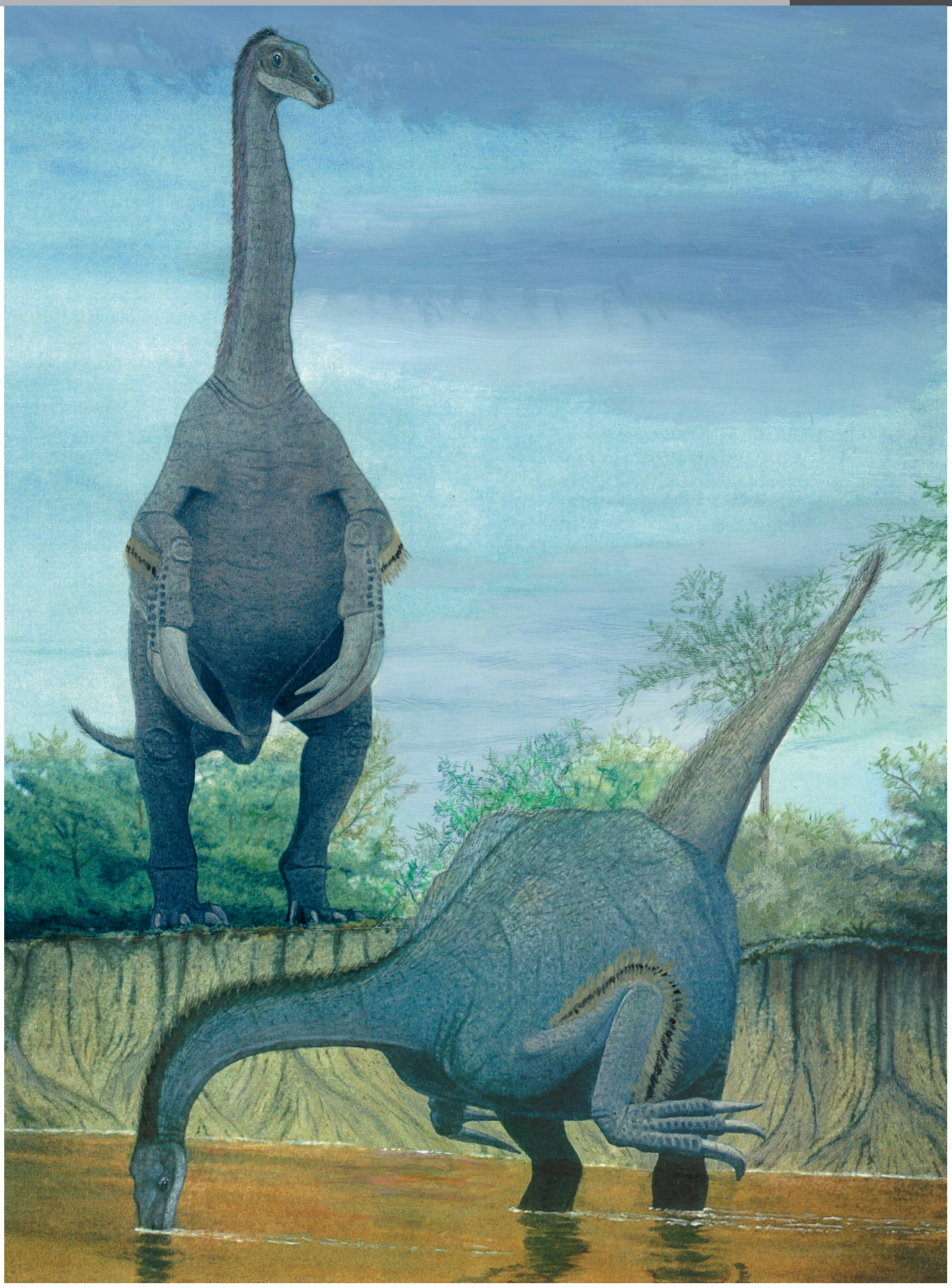
Erlikosaurus andrewsi
— 4.5 m (15 ft) TL, 1.2 tonnes
FOSSIL REMAINS Complete skull.
ANATOMICAL CHARACTERISTICS Teeth smaller and more numerous than in *Segnosaurus*, cheeks well developed. Toe claws enlarged.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayenshiree Svita.
HABITS Used large clawed feet for defense as well as hands.
NOTES May include *Enigmosaurus mongoliensis*.

Therizinosaurus cheloniformis
— 10 m (33 ft) TL, 5–10 tonnes
FOSSIL REMAINS Arms and some claws, parts of the hind limb.
ANATOMICAL CHARACTERISTICS Arm up to 3.5 m (11 ft) long, bearing very long, saber-shaped claws that were 0.7 m (over 2 ft) in length without their original horn sheaths.
AGE Late Cretaceous, late Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.



composite derived *therizinosaur*

OPPOSITE:
Therizinosaurus cheloniformis



NOTES Lack of remains of main body hinders size estimation, is largest known airfoilan, another example of a very large, high-browsing theropod like *Gigantoraptor*, and the *Deinocheirus* that shared its habitat.

— ALVAREZSAURS

SMALL AVEAIRFOILANS FROM THE EARLY CRETACEOUS TO THE END OF THE DINOSAUR ERA, ASIA AND WESTERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Teeth reduced. Scapula blades slender, humeri short, stouter, and distally expanded. Legs and feet long and slender.
HABITS Main defense high speed.
NOTES Originally thought to be aveairfoilans very close to birds, but opinion that haplocheirids are basal alvarezsaurs suggested otherwise, probability that latter are not related revives probable bird relations and possible loss of flight of alvarezsaurs because of large sternums, fused wrists and hands, and retroverted pubes. If secondarily flightless, probably descended from long-tailed fliers. Limited distribution may reflect insufficient sampling.

— BANNYKIDS

SMALL ALVAREZSAURS OF THE EARLY CRETACEOUS FROM ASIA.

ANATOMICAL CHARACTERISTICS Pectoral crest of humeri not greatly enlarged.
NOTES Lack of skulls and pubes hinders analysis of habits and relationships.

Tugulusaurus faciles
— 2 m (7 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Thumb not enlarged.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Lianmuqin.

Bannykus wulatensis
— 2 m (7 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Thumb enlarged.
AGE Early Cretaceous, Barremian or Aptian.
DISTRIBUTION AND FORMATION/S North-central China; Bayingobi.

— ALVAREZSAURIDS

SMALL ALVAREZSAURS FROM THE EARLY CRETACEOUS TO THE END OF THE DINOSAUR ERA, ASIA AND WESTERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Snouts semitubular, teeth very numerous and small, postorbital bar incomplete as in birds. Necks slender. Arms very short, stout, with greatly enlarged pectoral crest, powerfully muscled, wrists and upper hands fused, hands reduced to one massive functional finger and robust claw. Pubes strongly retroverted, unbooted, legs and feet very long and slender.
HABITS Main defense very high speed.
NOTES Number of genera may be excessive. Limited distribution may reflect insufficient sampling.

Parvicursor remotus
— Adult size not certain
FOSSIL REMAINS Partial skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Pubis strongly retroverted, foot strongly compressed from side to side.
AGE Early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayenshiree Svita.
NOTES Originally thought to be a small adult.

Alvarezsaurus calvoi
— 1 m (3.3 ft) TL, 4 kg (9 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Foot not strongly compressed from side to side.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Bajo de la Carpa.
NOTES *Achillesaurus manazzonei* probably the adult of this species.

Patagonykus puertai
— 1.9 m (6 ft) TL, 28 kg (60 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Pubis not strongly retroverted.
AGE Late Cretaceous, Turonian or Coniacian.
HABITAT/S Well-watered woodlands with short dry season.
DISTRIBUTION AND FORMATION/S Western Argentina; Rio Neuquén.

Linhenykus monodactylus
— 0.5 m (1.6 ft) TL, 0.5 kg (1.1 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; Wulansuhai.
HABITAT/S Semidesert with some dunes and oases.

Albertonykus borealis
— 1.1 m (3.5 ft) TL, 5 kg (12 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; upper Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

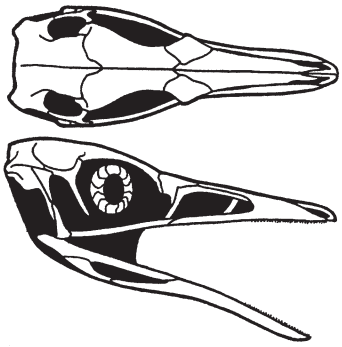
Ceratonykus oculatus
— 0.6 m (2 ft) TL, 2 kg (4 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Foot strongly compressed from side to side.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.

Xixianykus zhangi
— Adult size uncertain
FOSSIL REMAINS Minority of possibly juvenile skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Coniacian or Santonian.
DISTRIBUTION AND FORMATION/S Eastern China; Majiacun.

Shuvuuia deserti
— 0.7 m (2.3 ft) TL, 1.5 kg (3 lb)
FOSSIL REMAINS Two nearly complete skulls and several partial skeletons, external fibers.
ANATOMICAL CHARACTERISTICS Pubis strongly retroverted, foot strongly compressed from side to side. Short, hollow fibers on head and body.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.
HABITAT/S Desert with dunes and oases.

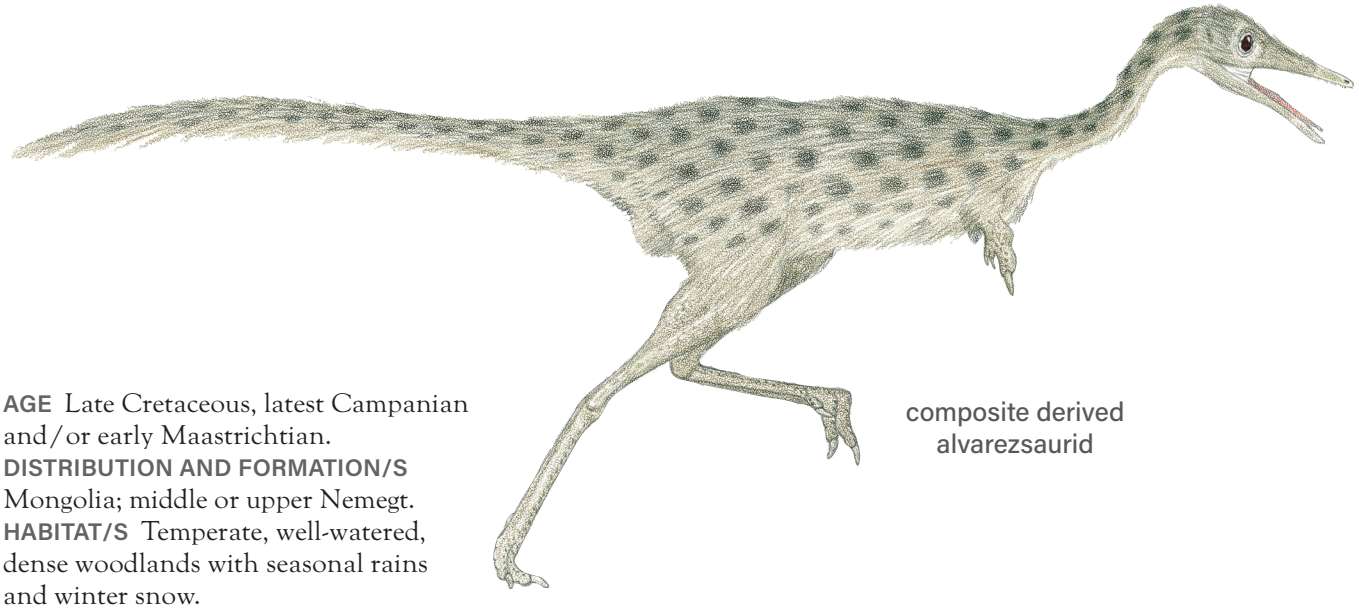
Nemegtonykus citus
— 1 m (3.3 ft) TL, 4.1 kg (9 lb)
FOSSIL REMAINS Two partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

Mononykus olecranus
— 1 m (3.3 ft) TL, 4.1 kg (9 lb)
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.



Shuvuuia deserti

composite derived alvarezsaurid
(see also next page)



composite derived alvarezsaurid

AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; middle or upper Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

— OVIRAPTOROSAURIFORMS

SMALL TO LARGE FLYING AND FLIGHTLESS HERBIVOROUS OR OMNIVOROUS AVEAIRFOILANS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly variable. Heads not large, short and deep, sides of back of head made of slender struts, postorbital bar complete, many bones including lower jaws fused together and extra joint absent, jaw joints highly mobile to allow complex chewing motion, teeth reduced or absent. Necks fairly long, ribs usually so short they do not overlap, increasing flexibility of neck. Trunks short. Tails short. Arms short to very long, fingers three to two. Legs short to very long.
HABITS Omnivorous or herbivorous, picked up small animals at least on occasion.
NOTES Omnivoropterygids, oviraptorosaurs, and avians and their common ancestor, operative only if three groups form a clade that excludes all other dinosaurs.

— OMNIVOROPTERYGIDS

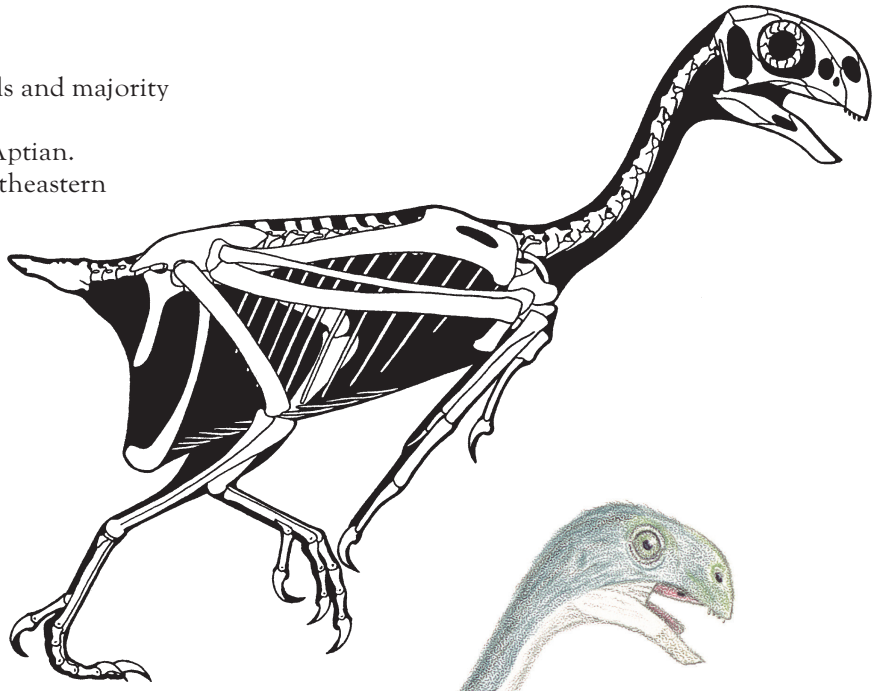
SMALL FLYING OVIRAPTOROSAURS LIMITED TO THE EARLY CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Lower jaws shallow, a few procumbent, small, pointed teeth at front of upper jaws. No uncinate processes on ribs. Vertebrae at tip of very short tails fused into a pygostyle. Sternal plates and ossified sternal ribs may be absent, very long arms and hands indicate very large wings, outer fingers severely reduced so there are only two fully functional fingers. Pubes a little retroverted, pelves broad, legs short and not as strong as arms, toes long, hallux reversed. Wings very large, tail feather fans present, ankle feathers in some fossils.
HABITS Capable of low-grade powered gliding, and possibly soaring flight superior to that of *Archaeopteryx*. Good climbers. Defense included climbing and flight. Probably diurnal.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.
NOTES A very oviraptorosaur-like skull strongly suggests a close relationship. Although not the direct ancestors of oviraptorosaurs, omnivoropterygids may represent the parrot-headed, short-tailed flying basal birds that oviraptorosaurs evolved from. Irregular presence of ankle feathers may indicate display rather than aerodynamic function. Specific diets difficult to determine because of the unusual configuration of head and jaws.

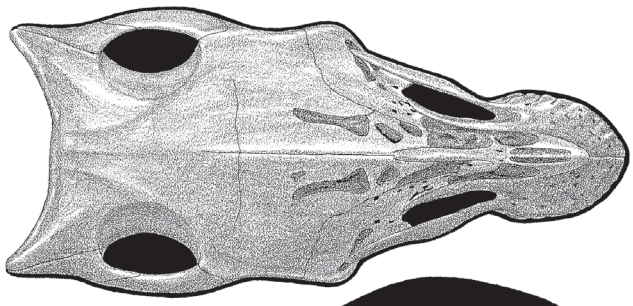
Sapeornis unnamed species?

— Adult size uncertain
FOSSIL REMAINS Complete but distorted skull with skeleton, extensive feathers.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Probably a species different from, and may be ancestral to, later *S. chaoyangensis*.

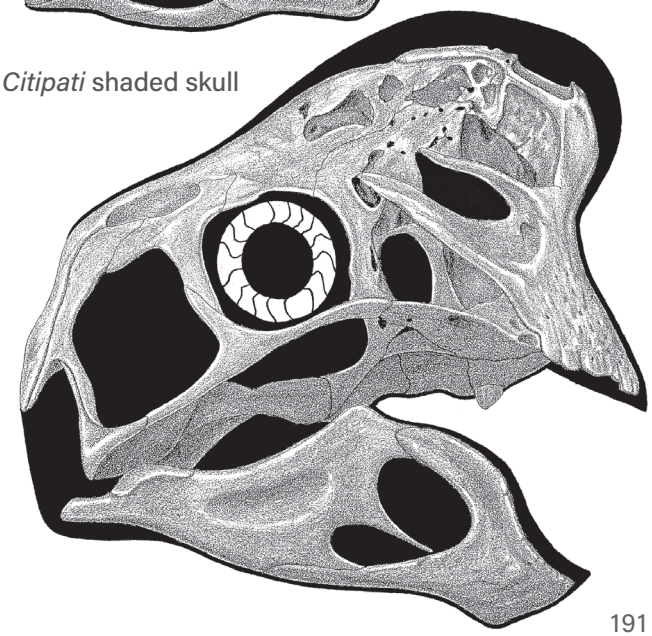
Sapeornis chaoyangensis
— 0.4 m (1.3 ft) TL, 1 kg (2 lb)
FOSSIL REMAINS Several complete skulls and majority of skeletons, feathers, gizzard stones.
AGE Early Cretaceous, early or middle Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES A much more common component of the fauna than the preceding species, probably includes *Omnivoropteryx sinousaorum*, *Didactylornis jii*, and a number of other species.



Sapeornis chaoyangensis



Citipati shaded skull



— OVIRAPTOROSAURS

SMALL TO LARGE HERBIVOROUS OR OMNIVOROUS AVEAIRFOILANS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly variable. Heads at least fairly short and deep, with parrot-like beaks. Arms short to moderately long, fingers three to two. Pubes moderately retroverted to usually vertical or procumbent, legs moderately to very long.
HABITS Defense included biting with beaks, slashing with hand claws, and evasion.
NOTES Presence of large ossified sternal plates, ossified sternal ribs, ossified uncinate processes, short tails in most examples, reduction of outer fingers in some examples, and pubic retroversion in basal examples strongly imply that the

flightless oviraptorosaurs were the secondarily flightless relatives of known flying omnivoropterygids; this requires significant but not massive reversals of some sections of the skeleton to a nonavian condition; protarchaeopterygids, avimimids, caudipterids, and caenagnathoids may have evolved collectively or independently from earlier fliers. Alternatively, omnivoropterygids were the flying descendants of oviraptorosaurs. In the conventional scenario the two groups were not closely related, in which case the heads and hands evolved in a remarkably convergent manner despite the lack of a common flight heritage. Fragmentary remains may record presence in Australia.

— PROTARCHAEOPTERYGIDS

SMALL OVIRAPTOROSAURS LIMITED TO THE EARLY CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Highly uniform. Heads not as deep as in other oviraptorosaurs, subrectangular, roof of mouth projects below rim of upper jaws, lower jaws shallow, frontmost teeth enlarged and well worn, rest of teeth small, blunt, and unserrated, teeth absent from tip of lower jaws. Skeletons lightly built. Large sternal plates present, arms long, three finger claws are large hooks. Pubes at least sometimes retroverted, legs long.
HABITS Divergence in tooth size and form is much greater than in other theropods. Incisor-like front teeth are reminiscent of rodents and imply gnawing on some form of hard plant material. Both climbing and running performance appear to be high, main defense climbing, high speed, and biting.
NOTES That these basal oviraptorosaurs are more birdlike than more-derived oviraptorosaurs is compatible with the group being secondarily flightless.

Protarchaeopteryx (or *Incisivosaurus*) *gauthieri*

— 0.8 m (2.7 ft) TL, 2 kg (5 lb)
FOSSIL REMAINS Almost complete skull and small minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group, number of teeth differs from *P. robusta*.
AGE Early Cretaceous, latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES May be direct ancestor of *P. robusta*.

Protarchaeopteryx robusta

— 0.7 m (2.3 ft) TL, 1.7 kg (3.7 lb)
FOSSIL REMAINS Majority of badly damaged skull and skeleton, some feathers.
ANATOMICAL CHARACTERISTICS Pubis appears to be at least somewhat retroverted. Tail feathers fairly long, vanes asymmetrical.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Arms not long enough and arm feathers too symmetrical for flight.
NOTES Misnamed as a closely related predecessor to the much earlier deinonychosaur *Archaeopteryx*. Pubic orientation ambiguous. May be direct ancestor of *P. ganqi*.

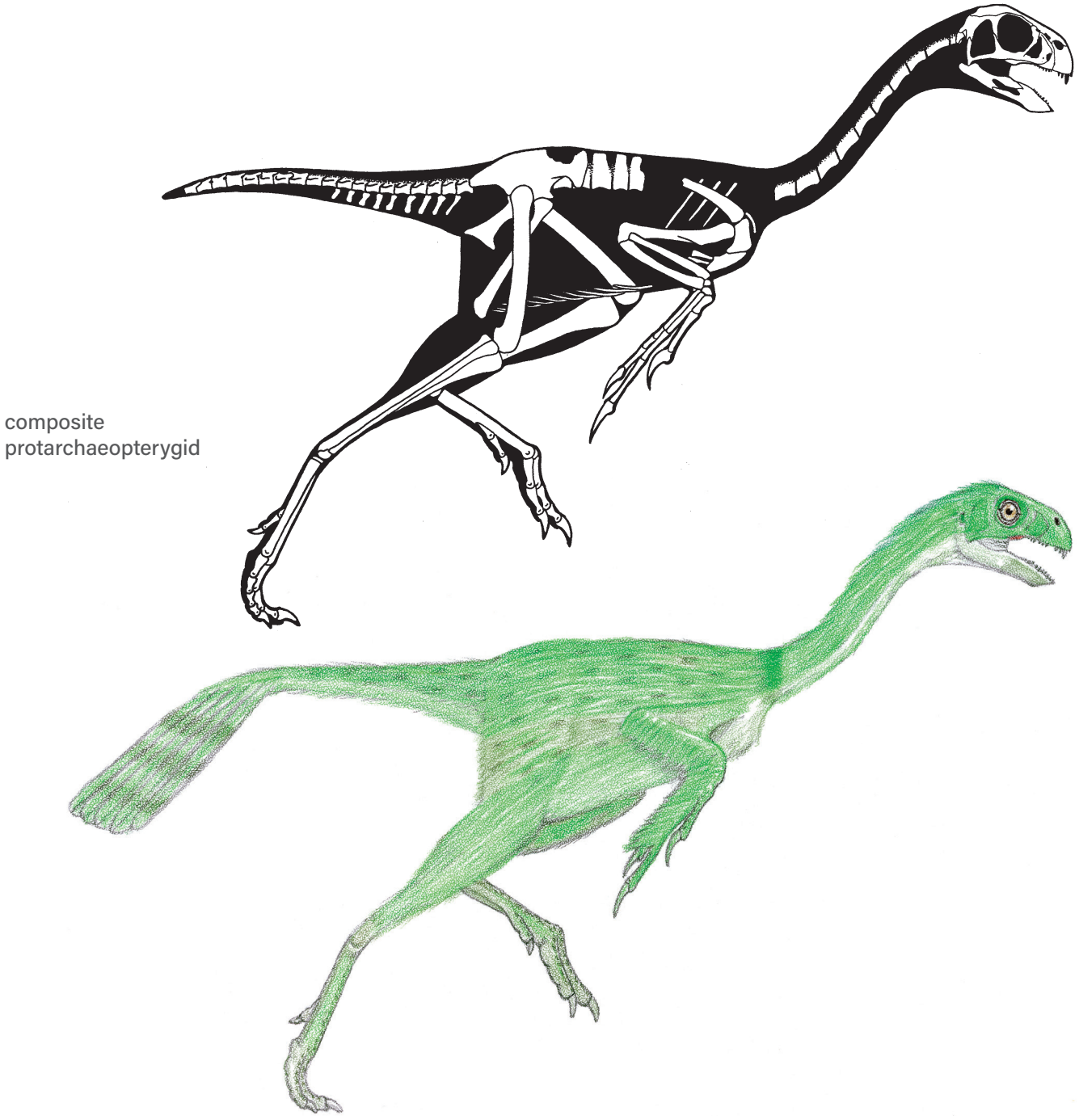
Protarchaeopteryx (or *Xingtianosaurus*) *ganqi*

— 0.7 m (2.3 ft) TL, 1.7 kg (3.7 lb)
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Arms shorter than in *P. robusta*. Pubis moderately retroverted.
AGE Early Cretaceous, earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Pubis clearly preserved in a retroverted posture; that pubic process of ilium is not retroverted is not incompatible with pubic retroversion because such is seen in some other dinosaurs. Elongated hand, pelvic characters, and not highly elongated lower limb indicate is a protarchaeopterygid rather than a caudipterid.

— CAUDIPTERIDS

SMALL OVIRAPTOROSAURS LIMITED TO THE EARLY CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Heads small, subtriangular, lower jaws shallow, a few procumbent, small, pointed teeth at front of upper jaws. Skeletons lightly built. Trunks short, uncinate processes on ribs. Ossified sternal plates and sternal ribs present, arms short, outer fingers severely reduced so there are only two fully functional fingers, claws not large. Pelves very large, pubes vertical, legs very long and gracile, leg muscles exceptionally well developed, semireversed hallux small, so speed potential very high.
HABITS Climbing ability low or nonexistent, main defense high speed.
NOTES That these basal oviraptorosaurs are more birdlike in certain regards than more-derived oviraptorosaurs is compatible with the group being secondarily flightless.



Caudipteryx zoui

— 0.65 m (2 ft) TL, 2.5 kg (5 lb)

FOSSIL REMAINS A number of complete skulls and skeletons, extensive feathers, bundles of gizzard stones.

ANATOMICAL CHARACTERISTICS Pygostyle not present. Well-developed feather fan on hand, possibly split fan at end of tail, latter showing pigment banding, large pennaceous feathers symmetrical, simpler feathers covering much of body.

AGE Early Cretaceous, latest Barremian and/or earliest Aptian.

DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.

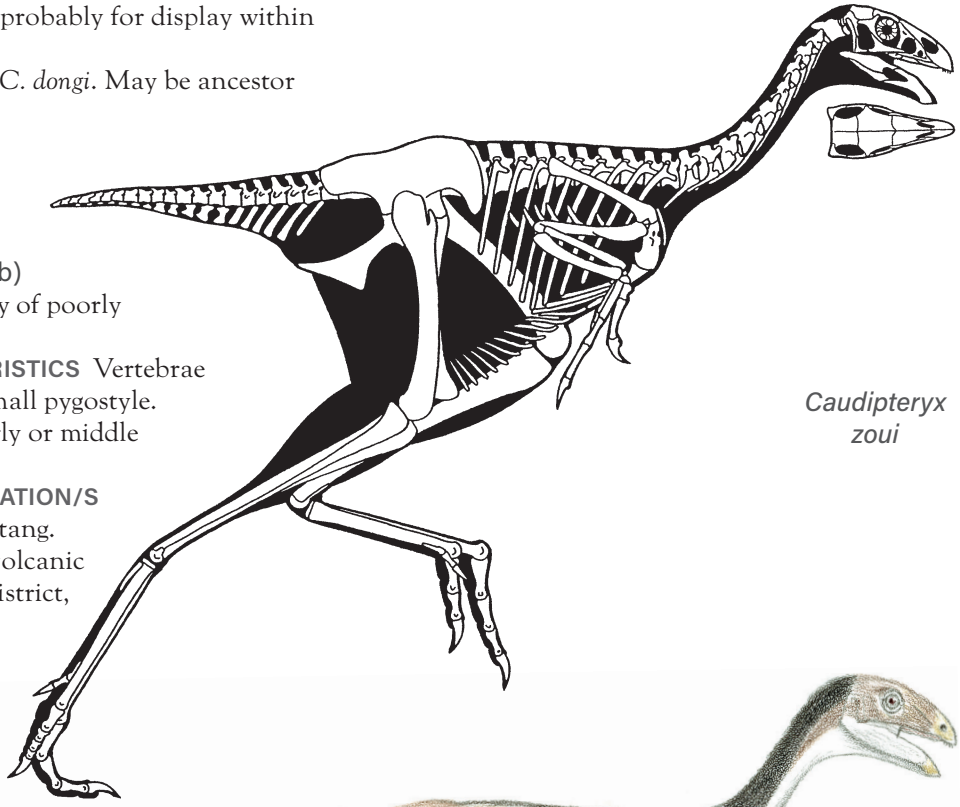
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

HABITS Presence of some small, sharp teeth imply *Caudipteryx* may have caught small animals, but gizzard stones verify diet of plants that required grinding. Small

hand and tail feather fans probably for display within the species.
NOTES Probably includes *C. dongi*. May be ancestor of *C. yixianensis*.

Caudipteryx (= *Similicaudipteryx*) *yixianensis*

— 1 m (3 ft) TL, 9 kg (20 lb)
FOSSIL REMAINS Majority of poorly preserved skeleton.
ANATOMICAL CHARACTERISTICS Vertebrae at tip of tail fused into a small pygostyle.
AGE Early Cretaceous, early or middle Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

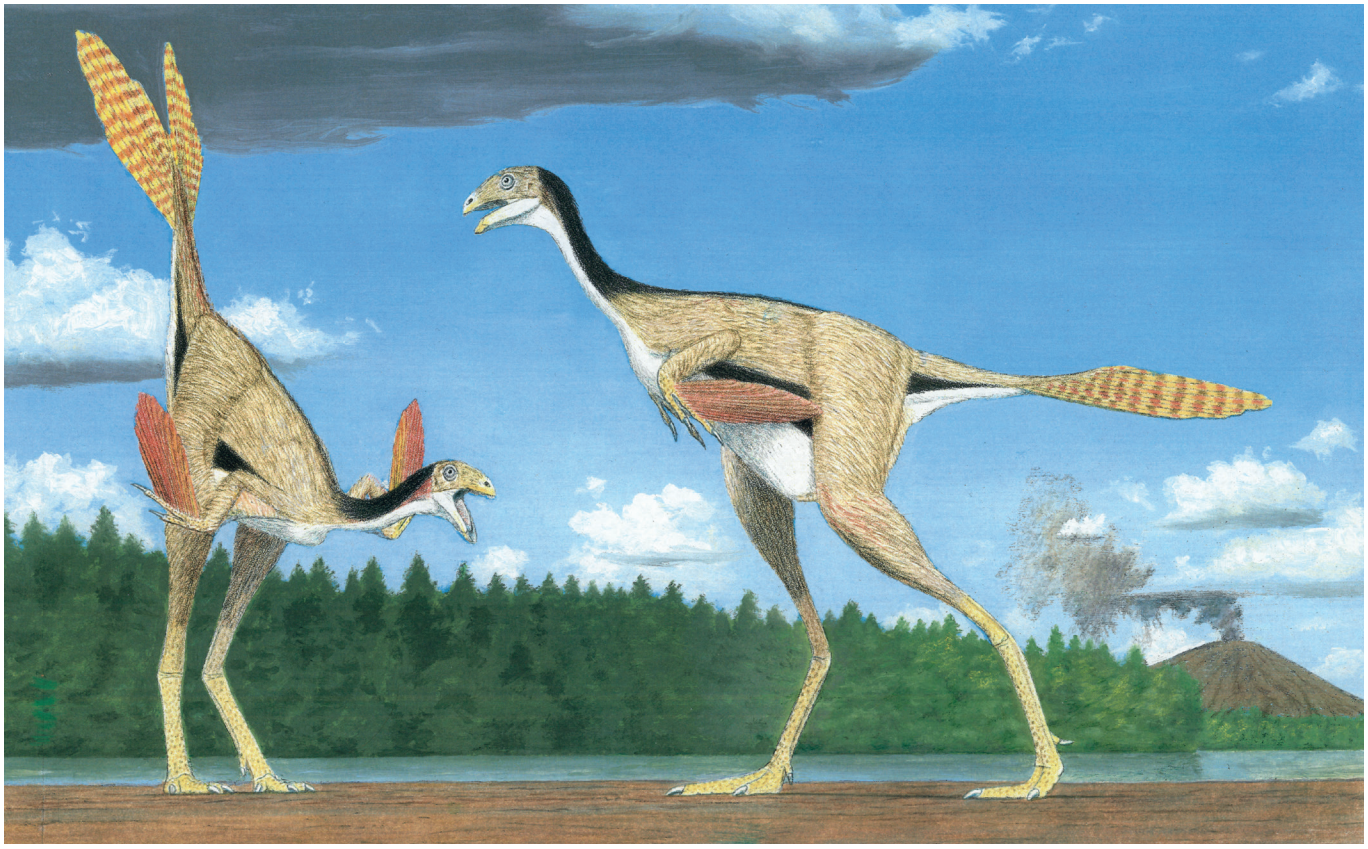


Caudipteryx zoui

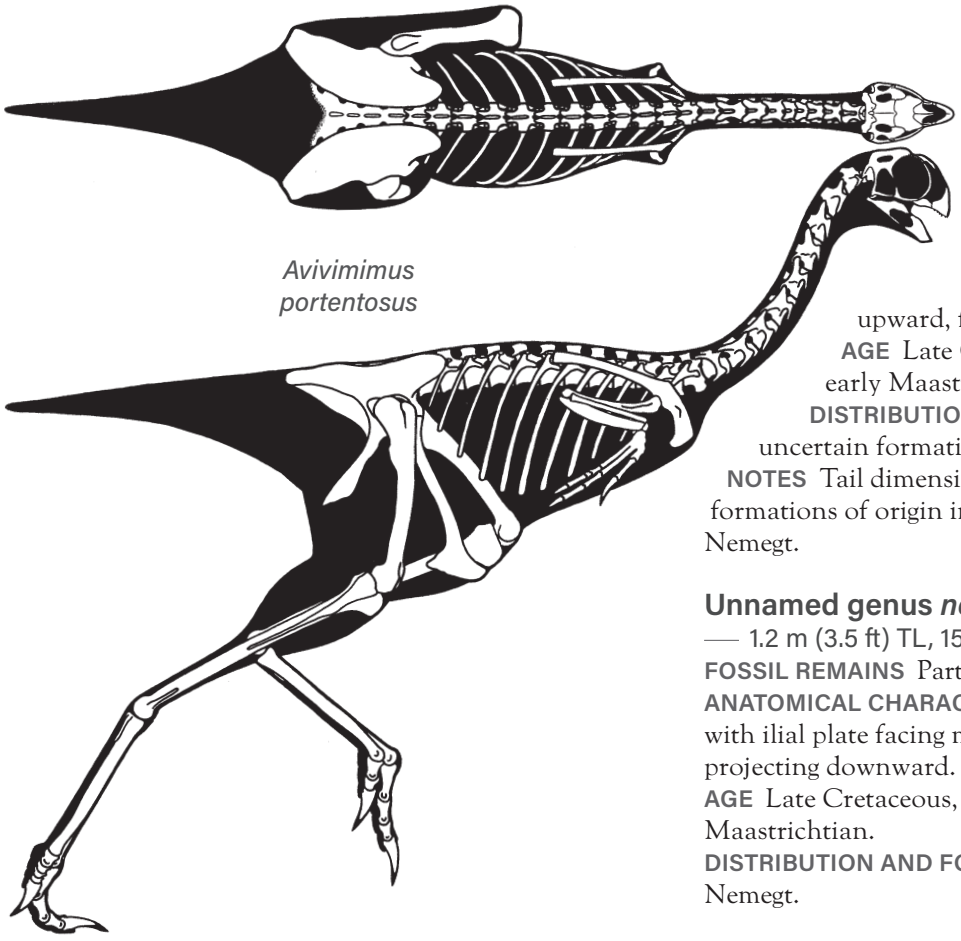
— AVIMIMIDS

SMALL OVIRAPTOROSAURS LIMITED TO THE LATE LATE CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Heads short, deep, broad aft, top of aft head somewhat bulbous, lower jaws fairly deep, small teeth at front of upper jaws. Arms short. Pelves large, pubes procumbent, legs very long and muscles exceptionally well developed, feet very long and strongly compressed from side to side, hallux absent and toes short, so speed potential very high.
HABITS Broad hips indicate large belly for processing plant material. Main defense high speed.



Caudipteryx zoui



Avivimimus portentosus

Avimimus portentosus

1.2 m (3.5 ft) TL, 14 kg (30 lb)

FOSSIL REMAINS Partial skulls and skeletons.

ANATOMICAL CHARACTERISTICS Skeleton highly fused incuding upper hand. Pelvis very broad with ilial plate facing strongly upward, forward end rounded.

AGE Late Cretaceous, later Campanian or early Maastrichtian.

DISTRIBUTION AND FORMATION/S Mongolia; uncertain formation.

NOTES Tail dimensions not yet detailed. Possible formations of origin include Djadokhta, Barun Goyot, Nemegt.

Unnamed genus *nemegtensis*

— 1.2 m (3.5 ft) TL, 15 kg (30 lb)

FOSSIL REMAINS Partial skulls and skeletons in bone bed.

ANATOMICAL CHARACTERISTICS Pelvis breadth normal with ilial plate facing mainly sideways, forward prong projecting downward.

AGE Late Cretaceous, late Campanian and/or earliest Maastrichtian.

DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.

HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

NOTES Placement in *Avimimus* incorrect because pelvis is so different.

— CAENAGNATHOIDS

SMALL TO LARGE OVIRAPTOROSAURS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Most or all adults with cassowary-like head crests, teeth absent, and blunt beaks present. Uncinate processes on ribs. Ossified sternal plates and sternal ribs present. Three finger claws well developed. Pubes vertical or procumbent. Olfactory bulbs reduced. Eggs highly elongated.
HABITS Pneumatic head crests too delicate for butting, for visual display within species. Defense included running, climbing, hand claws, and biting. Eggs formed and laid in pairs in flat, two-layered rings, partly exposed, probably by more than one female in each nest, brooded and incubated by adult sitting in empty center of nest with feathered arms and tail draped over eggs.

— CAENAGNATHIDS

SMALL TO LARGE OVIRAPTOROSAURS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly uniform. Lower jaws not very deep. Arms and hands long. Legs fairly long.

Microvenator celer
— Adult size uncertain
FOSSIL REMAINS Partial skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, middle Albian.
DISTRIBUTION AND FORMATION/S Montana; upper Cloverly.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Hagryphus giganteus
— 2 m (6.5 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Small portion of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Utah; middle Kaiparowits.

Caenagnathasia martinsoni
— 0.6 m (2 ft) TL, 1.5 kg (3 lb)
FOSSIL REMAINS Minority of two skulls.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Turonian or Coniacian.
DISTRIBUTION AND FORMATION/S Uzbekistan; Bissekty.

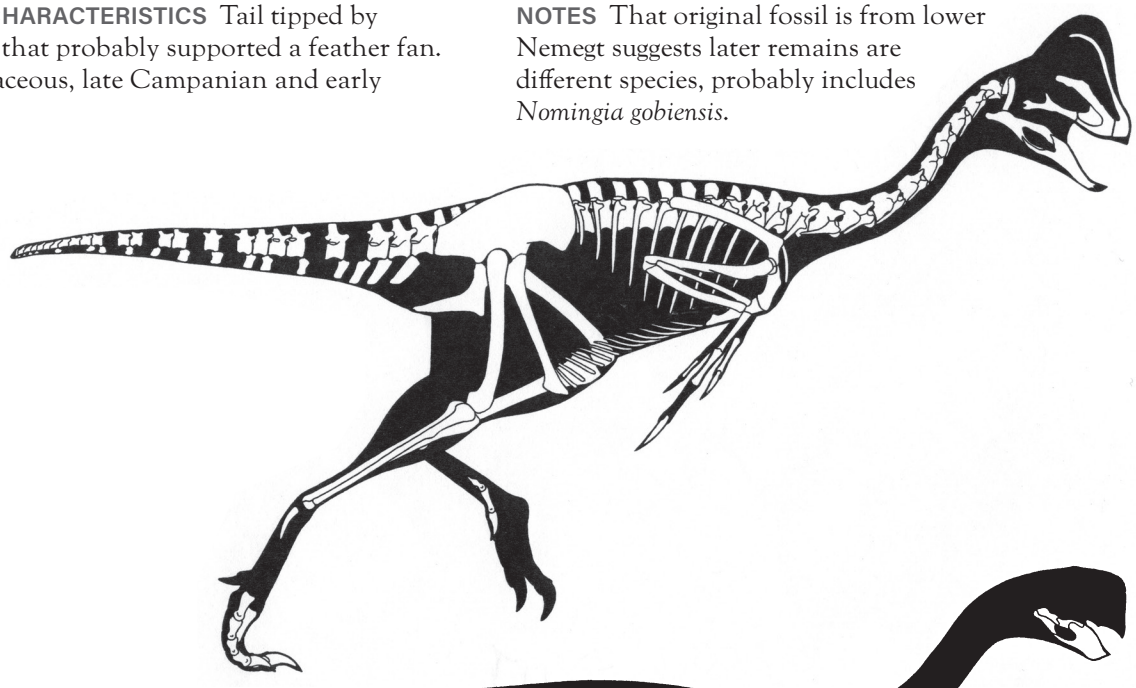
Chirostenotes pergracilis
— 3 m (10 ft) TL, 200 kg (400 lb)
FOSSIL REMAINS Assorted fragmentary remains.
ANATOMICAL CHARACTERISTICS Lower jaw shallow.
AGE Late Cretaceous, late middle and/or early to middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; Dinosaur Park, level uncertain.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Fragmentary remains of varying ontogenetic ages and uncertain stratigraphy of original fossils leave taxonomy uncertain, genus and species may or may not include juvenile *Chirostenotes* (= *Citipati*) *elegans*, *Caenagnathus collinsi*, *Macrophalangia canadensis*. May include ancestor of *Chirostenotes pennatus*.

Chirostenotes (or *Apatoraptor*) *pennatus*
— 1.5 m (5 ft) TL, 25 kg (50 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Usual placement in much earlier *C. pergracilis* not correct. May be an ancestor of *Anzu wyliei*.

Anzu wyliei
— 3.75 m (12 ft) TL, 265 kg (580 lb)
FOSSIL REMAINS Majority of a few skulls and skeletons.
ANATOMICAL CHARACTERISTICS Tall, broad head crest. Leg long.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S South Dakota; Hell Creek.
HABITAT/S Well-watered coastal woodlands.
NOTES Was usually included in much earlier *Chirostenotes pergracilis*.

Elmisaurus rarus

— 1.7 m (5.5 ft) TL, 20 kg (40 lb)
FOSSIL REMAINS Partial skeleton and other remains.
ANATOMICAL CHARACTERISTICS Tail tipped by short pygostyle that probably supported a feather fan.
AGE Late Cretaceous, late Campanian and early Maastrichtian?
DISTRIBUTION AND FORMATION/S Mongolia; at least lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
NOTES That original fossil is from lower Nemegt suggests later remains are different species, probably includes *Nomingia gobiensis*.



Anzu wyliei

Gigantoraptor erlianensis

— OVIRAPTORIDS

SMALL OVIRAPTOROSAURS LIMITED TO THE LATE LATE CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Uniform. Highly pneumatic heads subrectangular, snouts short, somewhat parrot-like beaks deep, nostrils above preorbital openings, blunt pair of pseudoteeth on strongly downward-projecting mouth roof, eyes not especially large, lower jaws deep. Outer two fingers subequal in length and robustness, finger claws well developed. Pubes vertical or procumbent, legs not slender.
HABITS The downward-jutting pseudoteeth indicate a crushing action.
NOTES The number of genera named in this group appears excessive in part because fossils without crests may be juveniles or females of crested species. Head crests were probably enlarged by keratin coverings.

Gigantoraptor erlianensis

— 8 m (25 ft) TL, 2.4 tonnes
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Hand slender.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Northern China; Iren Dabasu.
HABITAT/S Seasonally wet-dry woodlands.
HABITS Another example of a large, high-browsing theropod similar to *Deinocheirus* and *Therizinosaurus*. Better able to defend itself against predators than smaller oviraptors, also able to run away from predators.

NOTES Giant eggs up to 0.5 m (1.6 ft) long laid in enormous rings up to 3 m (10 ft) across, found in Asia, probably laid by big oviraptors such as *Gigantoraptor*.

Nankangia jiangxiensis

— 2.5 m (8 ft) TL, 85 kg (190 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern China; Nanxiong.

Yulong mini

— Adult size uncertain
FOSSIL REMAINS A few complete and partial juvenile skulls and skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Eastern China; Qiupa.

Oviraptor philoceratops

— 1.6 m (5 ft) TL, 25 kg (50 lb)
FOSSIL REMAINS Majority of poorly preserved skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head not as deep as in other oviraptorids, full extent of head crest uncertain. Hand large.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Presence of lizard skeleton in gut cavity of the skeleton indicates that the oviraptorid diet included at least some small animals.
NOTES Other oviraptorids were placed in *Oviraptor* until it was realized this is a very distinct genus.

Oviraptor philoceratops

Banji long

— 2.5 m (8 ft) TL, 85 kg (190 lb)
FOSSIL REMAINS Three nearly complete skulls and partial skeletons, adult to juvenile.
ANATOMICAL CHARACTERISTICS Head crest low arced.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern China; Nanxiong.
NOTES *Huanansaurus ganzhouensis* and *Tongtianlong limosus* may be more mature male and females of this taxon. One fossil preserved in position suggests that it died stranded in mud.

Corythoraptor (or *Citipati*) *jacobsi*

— 2.5 m (8 ft) TL, 85 kg (190 lb)
FOSSIL REMAINS Nearly complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Well-developed vertical crest.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern China; Nanxiong.

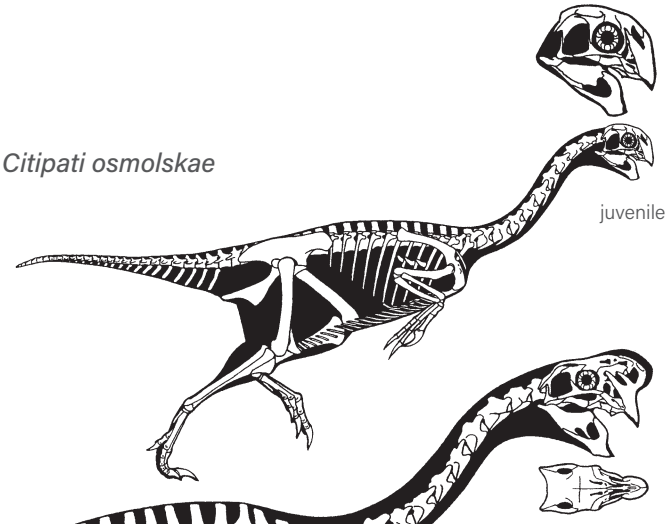
Citipati osmolskae

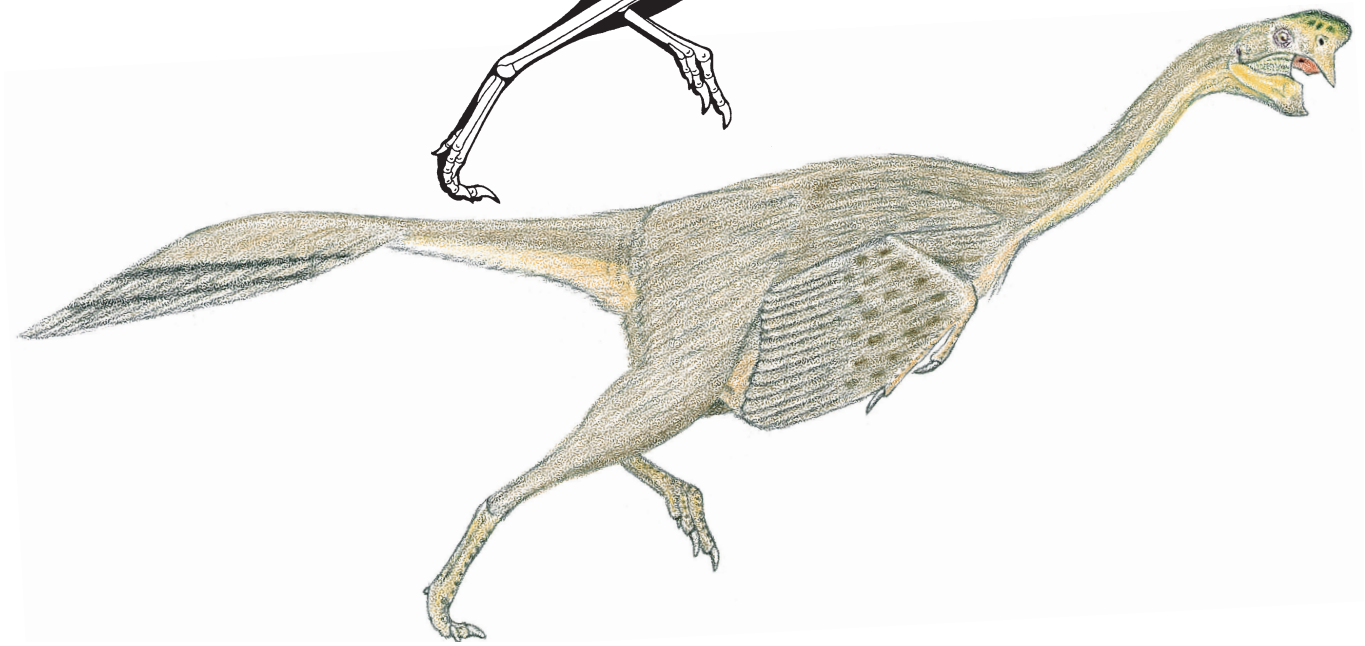
— 2.5 m (8 ft) TL, 85 kg (190 lb)
FOSSIL REMAINS Several complete and partial skulls and skeletons from embryo to adult, completely known, nests, some with adults in brooding posture on complete nests.
ANATOMICAL CHARACTERISTICS Well-developed crest projects forward above upper beak. Tail tipped by small pygostyle that probably supported a feather fan. Elongated eggs 18 cm (7 in) long.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Presence of remains of juvenile dinosaurs in some nests indicates that the oviraptorid diet included at least some small animals.
NOTES Showing that small, crestless *Khaan mckennai* is or is not the juvenile of this species requires examination of bone microstructure.

Banji long skulls growth series

Citipati osmolskae

juvenile





Rinchenia (or *Citipati*) *mongoliensis*

Rinchenia (or *Citipati*) *mongoliensis*
— 1.7 m (5.5 ft) TL, 25 kg (55 lb)
FOSSIL REMAINS Complete skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Subtriangular head crest very large.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; middle and/or upper Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

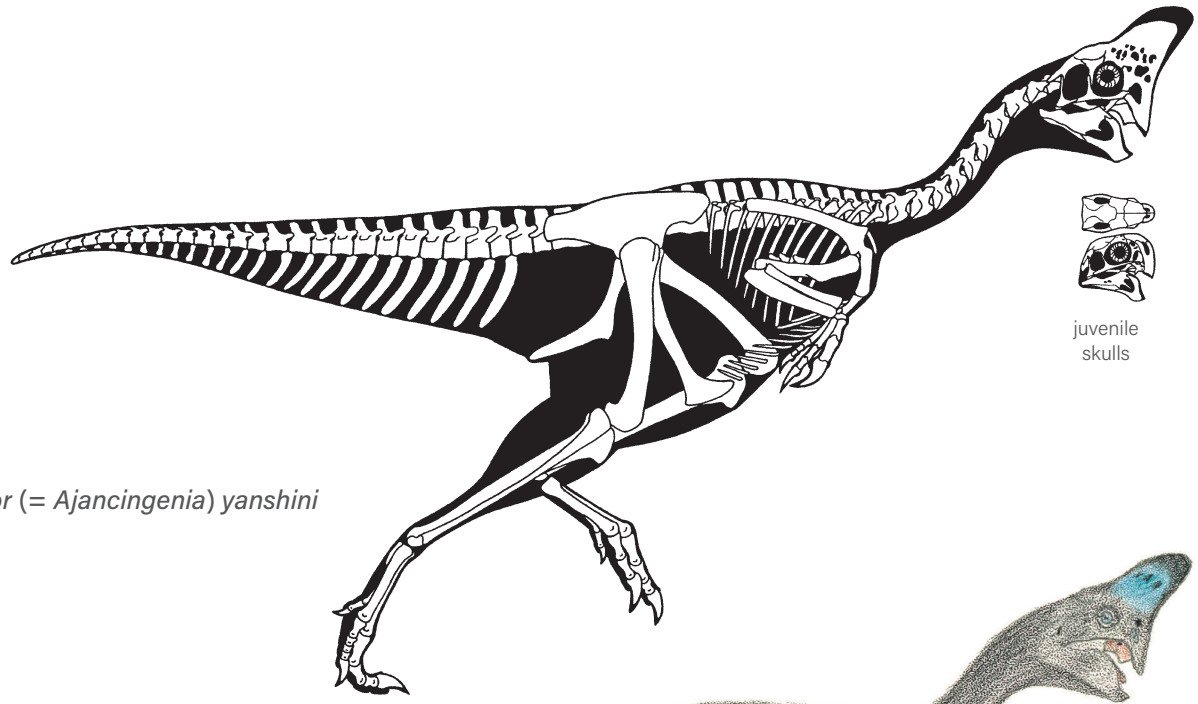
Wulatelong gobiensis
— 1.7 m (5.5 ft) TL, 25 kg (55 lb)
FOSSIL REMAINS Majority of poorly preserved skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Northwestern China; Wulansuhai.

Shixinggia oblita
— 2 m (7 ft) TL, 40 kg (85 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern China; Pingling.

Conchoraptor (= *Ajancingenia*) *yanshini*
— 1.5 m (5 ft) TL, 19 kg (40 lb)
FOSSIL REMAINS Complete and partial skulls and skeletons, adult and juvenile.
ANATOMICAL CHARACTERISTICS Very large forward-pointed head crest. Tail deep in at least one morph, tipped by short pygostyle that probably supported a feather fan. Thumb about as long as other fingers, hand robust at least in one morph.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.
HABITS Large thumb a weapon that may also have been used for feeding in some manner.
NOTES Showing that large, crested *C. gracilis* is or is not the adult of this species requires examination of bone microstructure. Original genus *Ingenia* preoccupied by an invertebrate. *Conchoraptor* has priority over more recent *Ajancingenia* if they are one genus. May be the ancestor of *C. barsboldi*.

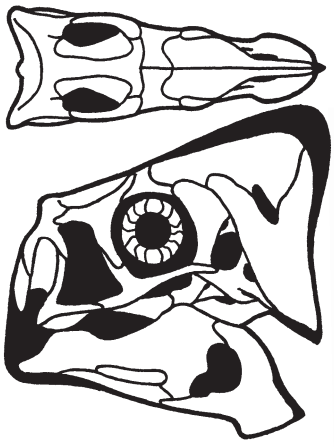
Conchoraptor (= *Nemegtomaia*) *barsboldi*
— 2 m (7 ft) TL, 45 kg (100 lb)
FOSSIL REMAINS Two poorly preserved complete skulls and minority of four skeletons.
ANATOMICAL CHARACTERISTICS Large crest above upper beak.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; middle and/or upper Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
NOTES Separation from the very similar *Conchoraptor* is not warranted.

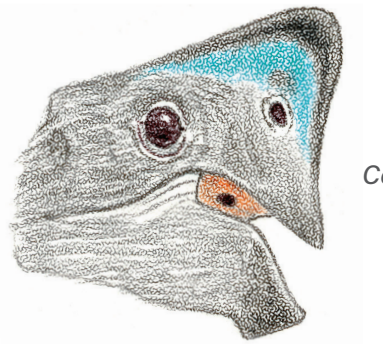
Conchoraptor (or *Heyuannia*) *huangi*
— 1.5 m (5 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Late Cretaceous.
DISTRIBUTION AND FORMATION/S Southern China; Dalangshan.
NOTES Available evidence insufficient to make separate genus from *Conchoraptor*.



juvenile skulls

Conchoraptor (= *Ajancingenia*) *yanshini*





Conchoraptor (= *Nemegtomaia*) *barsboldi*

SAUROPODOMORPHS

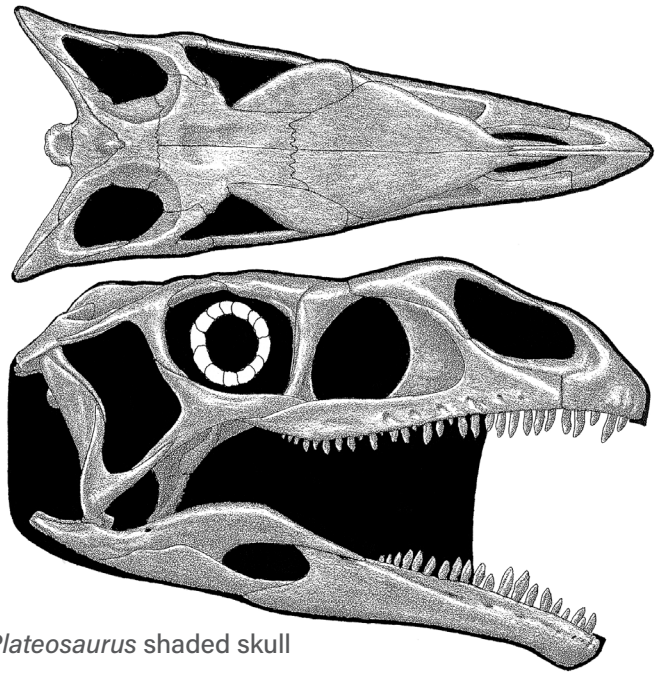
SMALL TO COLOSSAL HERBIVOROUS AND OMNIVOROUS SAURISCHIAN DINOSAURS FROM THE LATE TRIASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Moderately variable. Heads small, not strongly constructed, nostrils enlarged, teeth blunt, nonserrated. Necks long and slender. Tails long. Arms and legs neither elongated nor slender. Five fingers. Pelves small to large, five to four toes. Largely bipedal to always quadrupedal when moving, all able to rear up on hind legs. Brains reptilian. Gizzard stones sometimes present, used to help grind or stir up ingested food. In trackways hands usually farther from midline than feet, never closer, able to rear up with varying degrees of ease.
HABITAT Very variable, deserts to well-watered forests, tropics to polar regions.
HABITS Predominantly herbivorous browsers and grazers, although would have been prone to pick up and consume small animals; did not extensively chew food before swallowing. Main defense clawed feet and tails. Adept surface swimmers so able to cross large bodies of water.

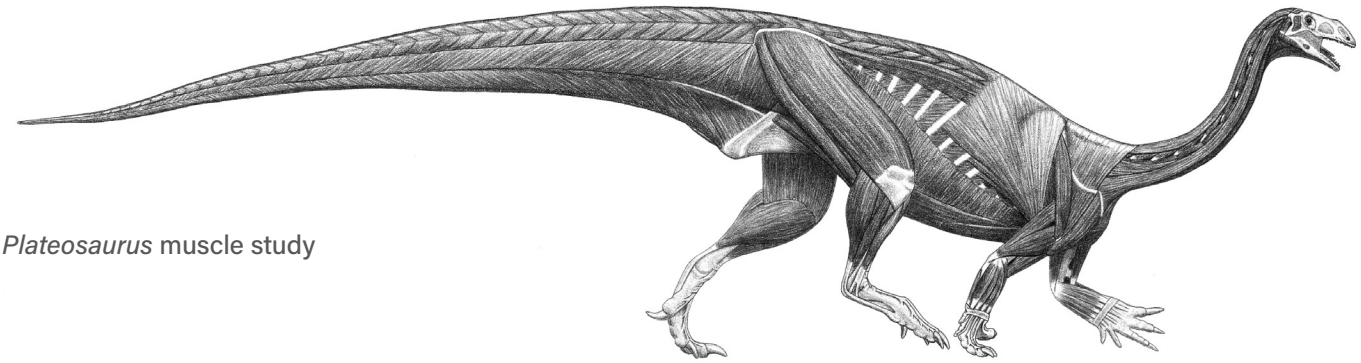
PROSAUROPODS

SMALL TO LARGE HERBIVOROUS AND OMNIVOROUS SAUROPODOMORPHS LIMITED TO THE LATE TRIASSIC AND EARLY JURASSIC, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads lightly built, top of snouts fairly broad across. Tails moderately long. Skeletons not pneumatic, respiratory system poorly understood except that birdlike system not present. Shoulder girdles not large, hands short and broad, grasping fingers fairly long, large claws usually present on most fingers, especially thumbs. Pelves short, pubes strongly procumbent, lower legs about as long as upper, feet fairly long, toes long and flexible, outermost toes very reduced. All able to slow walk quadrupedally, those with long arms mainly quadrupedal, with short arm mainly bipedal, or intermediate. Arms and legs flexed but not elongated or slender, so able to run at modest speeds.
ONTOGENY Growth rates moderate, variable within at least some species.
HABITATS Very variable, deserts to well-watered forests, tropics to poles.
HABITS Some or all may have been omnivores, preferred light vegetation. Main defense standing and lashing out with clawed hands and feet. Small prosauropods may have used clawed hands to dig burrows. May have had some diving ability.
ENERGETICS Thermophysiology probably intermediate, energy levels and food consumption probably low compared to more-derived dinosaurs.



Plateosaurus shaded skull



Plateosaurus muscle study

NOTES Fragmentary Early Jurassic *Glacialisaurus hammeri* demonstrates prosauropods dwelled in Antarctica. Whether all the many genera are justified is doubtful. This group is splittable into a number of subdivisions, but relationships within group and with sauropods are uncertain. Many researchers consider known prosauropods to be a sister group to sauropods, but others consider some or all of the first genera to be below the prosauropod-sauropod split, or the latter may have evolved from more-derived prosauropods. *Eoraptor* may be a very basal sauropodomorph. Based on supposedly Early Jurassic inadequate remains, Asian *Eshanosaurus deguchiianus* may be a prosauropod rather than a therizinosaur or other avepod.

BASO-PROSAUROPODS

SMALL PROSAUROPODS LIMITED TO THE LATE TRIASSIC.

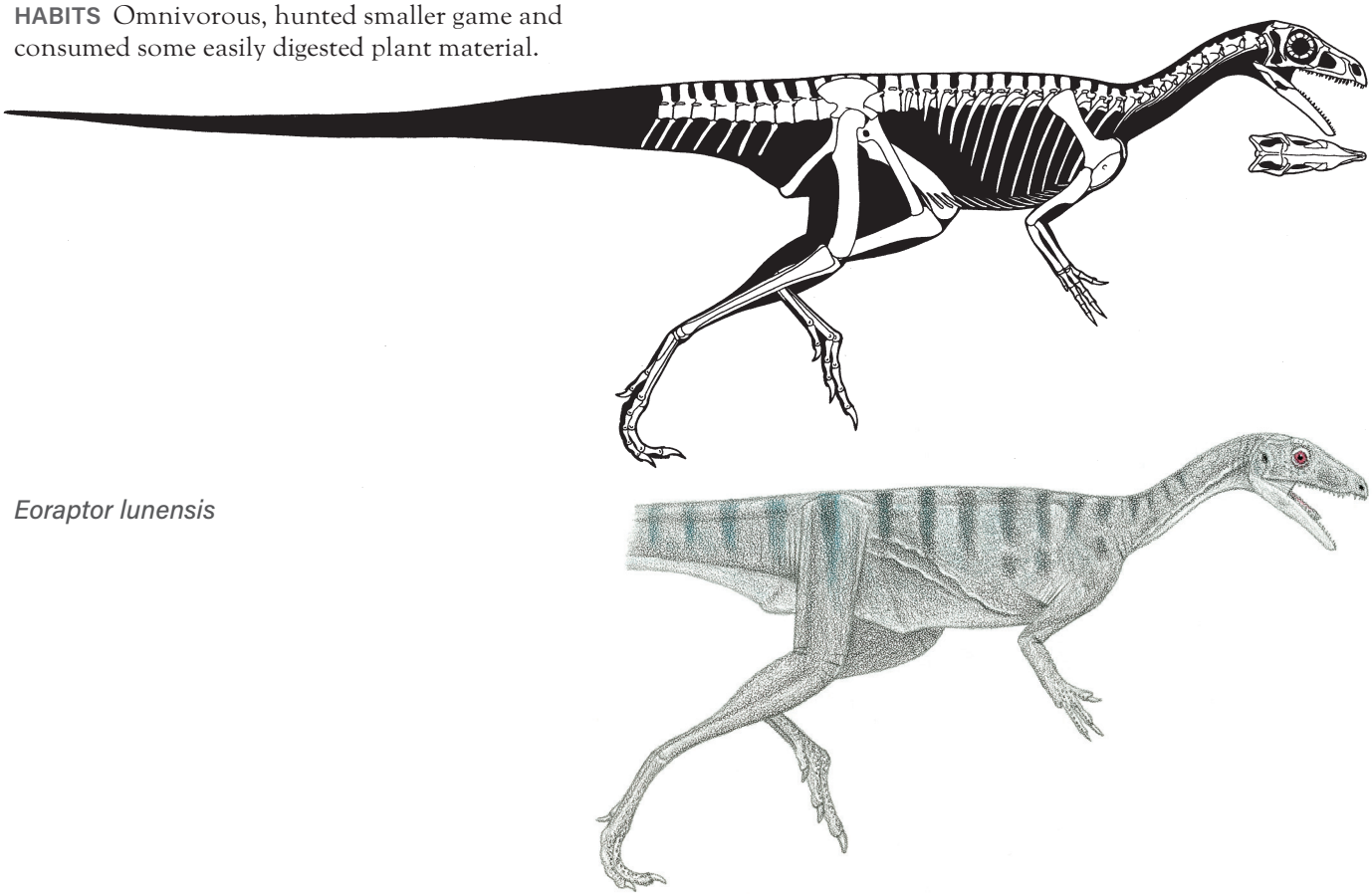
ANATOMICAL CHARACTERISTICS Lightly built. Often at least some teeth sharp. Necks neither markedly nor very slender. Thumbs not enlarged.
NOTES Baso-prosauropods and prosauropods excluding eusauropods. Limited distribution may reflect insufficient sampling.

Eoraptor lunensis

— 1.7 m (5.5 ft) TL, 4.7 kg (10 lb)
FOSSIL REMAINS Two nearly complete skulls and skeletons, almost completely known.
ANATOMICAL CHARACTERISTICS Back teeth bladed and serrated, front teeth more leaf shaped. Pubis procumbent.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Northern Argentina; lower Ischigualasto.
HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.
HABITS Omnivorous, hunted smaller game and consumed some easily digested plant material.
NOTES Has been considered a very basal saurischian, sauropodomorph, ornithoscelid, and/or theropod; the broad top of snout favors prosauropod status.

Mbiresaurus raathi

— 2.3 m (7.5 ft) TL, 15 kg (30 lb)
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Triassic, late? Carnian.
DISTRIBUTION AND FORMATION/S Zimbabwe; Pebbly Arkose.



Eoraptor lunensis

Guaibasaurus candelariensis
— 2 m (6.5 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, early Norian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Caturrita.
NOTES Originally thought to be a basotheropod.

Buriolestes schultzi
— 1.5 m (5 ft) TL, 4 kg (8 lb)
FOSSIL REMAINS Two skulls and partial skeletons, other remains.
ANATOMICAL CHARACTERISTICS Head shallow, fairly broad, front upper teeth fairly large, most small, most teeth bladed, front lower teeth project somewhat forward. Arm moderately short. Predominantly bipedal.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Southern Brazil; upper Santa Maria.
HABITS More omnivorous than euprosauropods.

Pampadromaeus barberenai
— 1.5 m (5 ft) TL, 4.1 kg (8 lb)
FOSSIL REMAINS Majority of skull and skeleton, possible additional partial remains including juvenile.
ANATOMICAL CHARACTERISTICS Most teeth bladed. Arm moderately short. Predominantly bipedal.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Southern Brazil; upper Santa Maria.
HABITS More predaceous than euprosauropods.

Panphagia protos
— 1.7 m (5.5 ft) TL, 6 kg (12 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Front lower teeth bladed. Arm moderately short. Predominantly bipedal.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Northern Argentina; lower Ischigualasto.
HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.
HABITS More predaceous than euprosauropods.

Saturnalia tupiniquim
— 1.5 m (5 ft) TL, 4 kg (8 lb)
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Arm moderately short. Predominantly bipedal.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Southern Brazil; upper Santa Maria.
NOTES *Nhandumirim waldsangae* may be juvenile of this species.

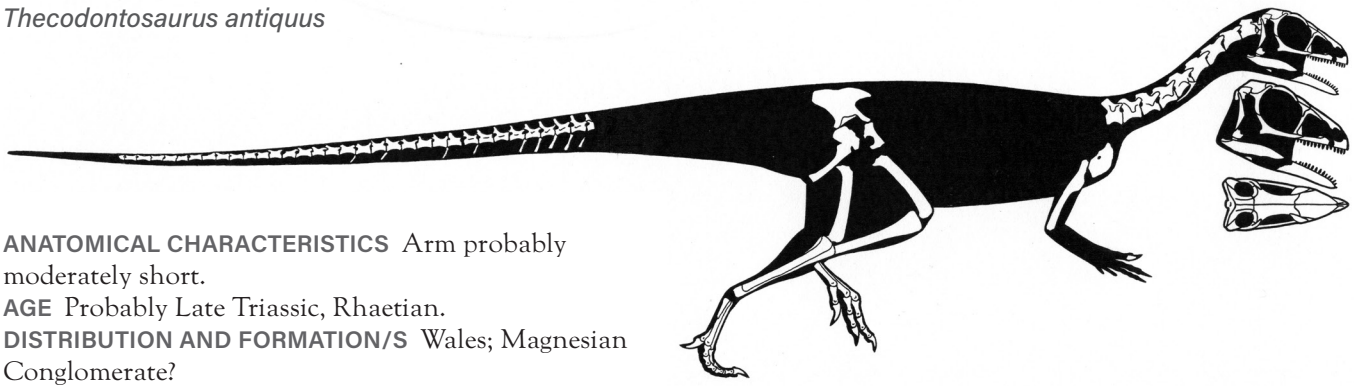
Bagualosaurus agudoensis
— 1.7 m (5.5 ft) TL, 6 kg (12 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; upper Santa Maria.

Thecodontosaurus antiquus
— 2.5 m (8 ft) TL, 20 kg (40 lb)
FOSSIL REMAINS Majority of skull and partial skeletons, adult to juvenile.

Buriolestes schultzi

Pampadromaeus barberenai

Thecodontosaurus antiquus



ANATOMICAL CHARACTERISTICS Arm probably moderately short.
AGE Probably Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S Wales; Magnesian Conglomerate?
HABITAT/S Island.
NOTES *Pantydraco caducus*, *Asylosaurus yalensis* probably immature examples of this species. Found in ancient fissure fills. Name incorrectly implies is among the basal archosaur thecodonts. Some of the remains destroyed in World War II by Axis bombing. May be example of island dwarfism.

EUPROSAUROPODS

SMALL TO LARGE HERBIVOROUS AND OMNIVOROUS PROSAUROPODS LIMITED TO THE LATE TRIASSIC AND EARLY JURASSIC, ALL CONTINENTS.

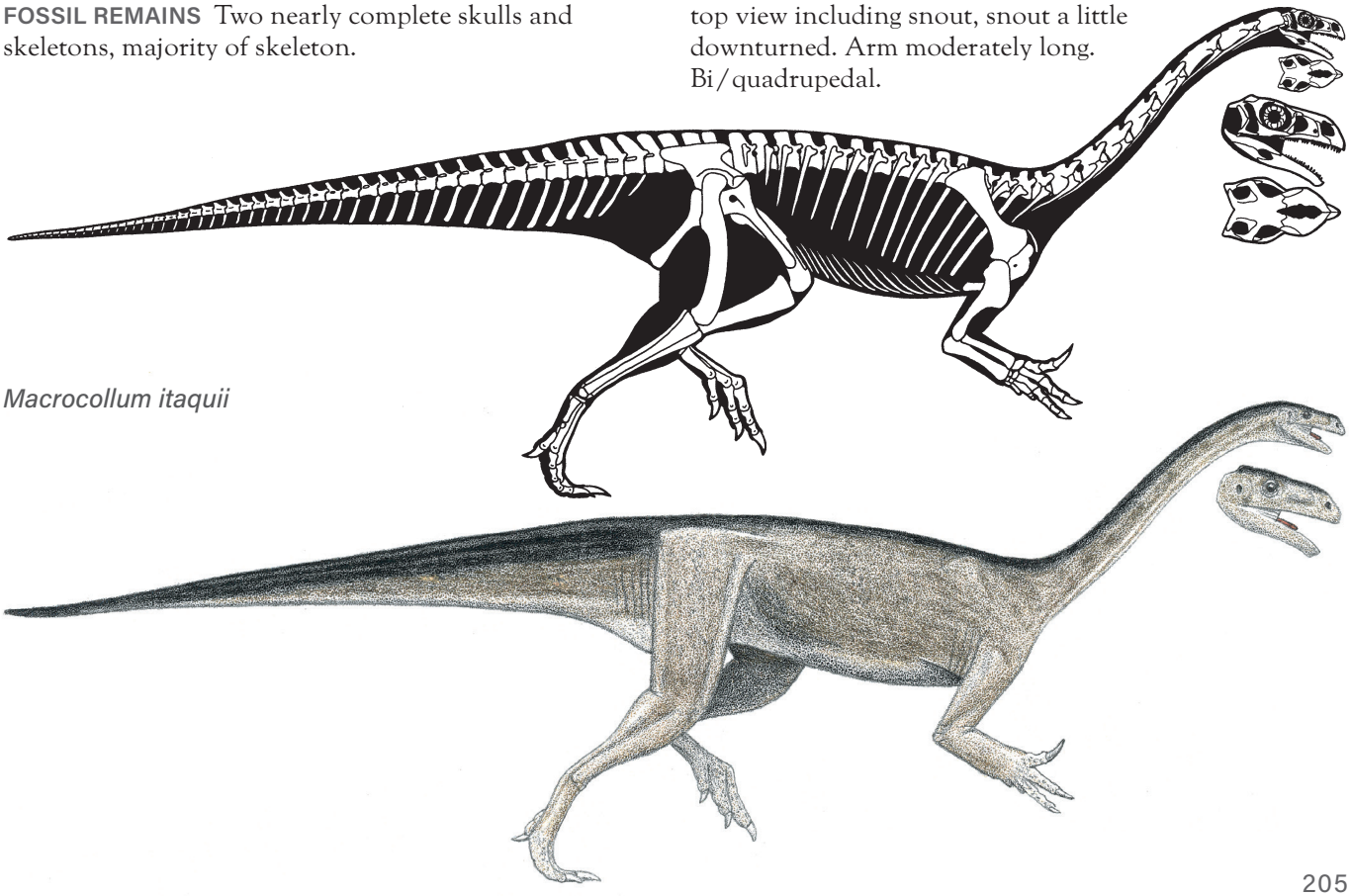
ANATOMICAL CHARACTERISTICS Stoutly built. Partial cheeks very probably present in at least some species, same for incipient beaks, antorbital fenestrae reduced, teeth blunt. Necks moderately long, quite slender. Trunks long. Thumbs and claws enlarged. Large claws on innermost toes.
HABITS First herbivores able to high browse, especially when rearing.
NOTES Euprosauropods are prosauropods with elongated, slender necks that include *Plateosaurus*.

Macrocollum itaquii

— 3.1 m (10 ft) TL, 90 kg (200 lb)
FOSSIL REMAINS Two nearly complete skulls and skeletons, majority of skeleton.

ANATOMICAL CHARACTERISTICS Head quite small, subrectangular in side view, broad in top view including snout, snout a little downturned. Arm moderately long. Bi/quadrupedal.

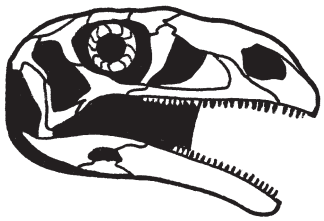
Macrocollum itaquii



AGE Late Triassic, early and/or middle Norian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Candelaria.

Unaysaurus tolentinoi
— Adult size uncertain
FOSSIL REMAINS Nearly complete skull and minority of skeleton, minority of juvenile skeleton.
ANATOMICAL CHARACTERISTICS Head shallow, subrectangular, snout a little downturned. Arm moderately long. Bi/quadrupedal.
AGE Late Triassic, early Norian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Caturrita.

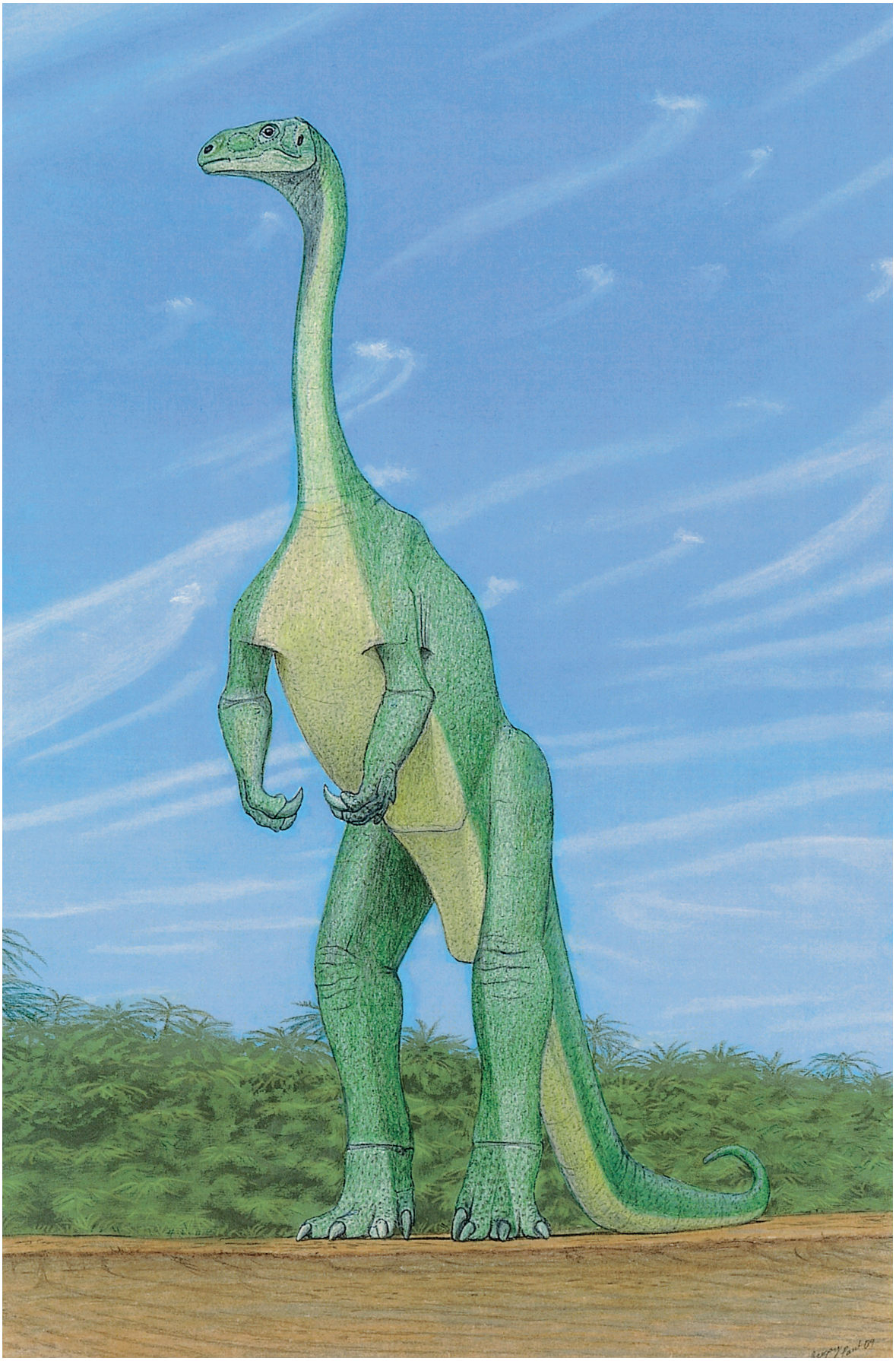
Plateosaurus (or *Issi*) *saaneq* (or *gracilis*)
— Adult size uncertain
FOSSIL REMAINS Majority of two skulls, immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Eastern Greenland; upper Malmros Klint.
NOTES May be *P. gracilis*.



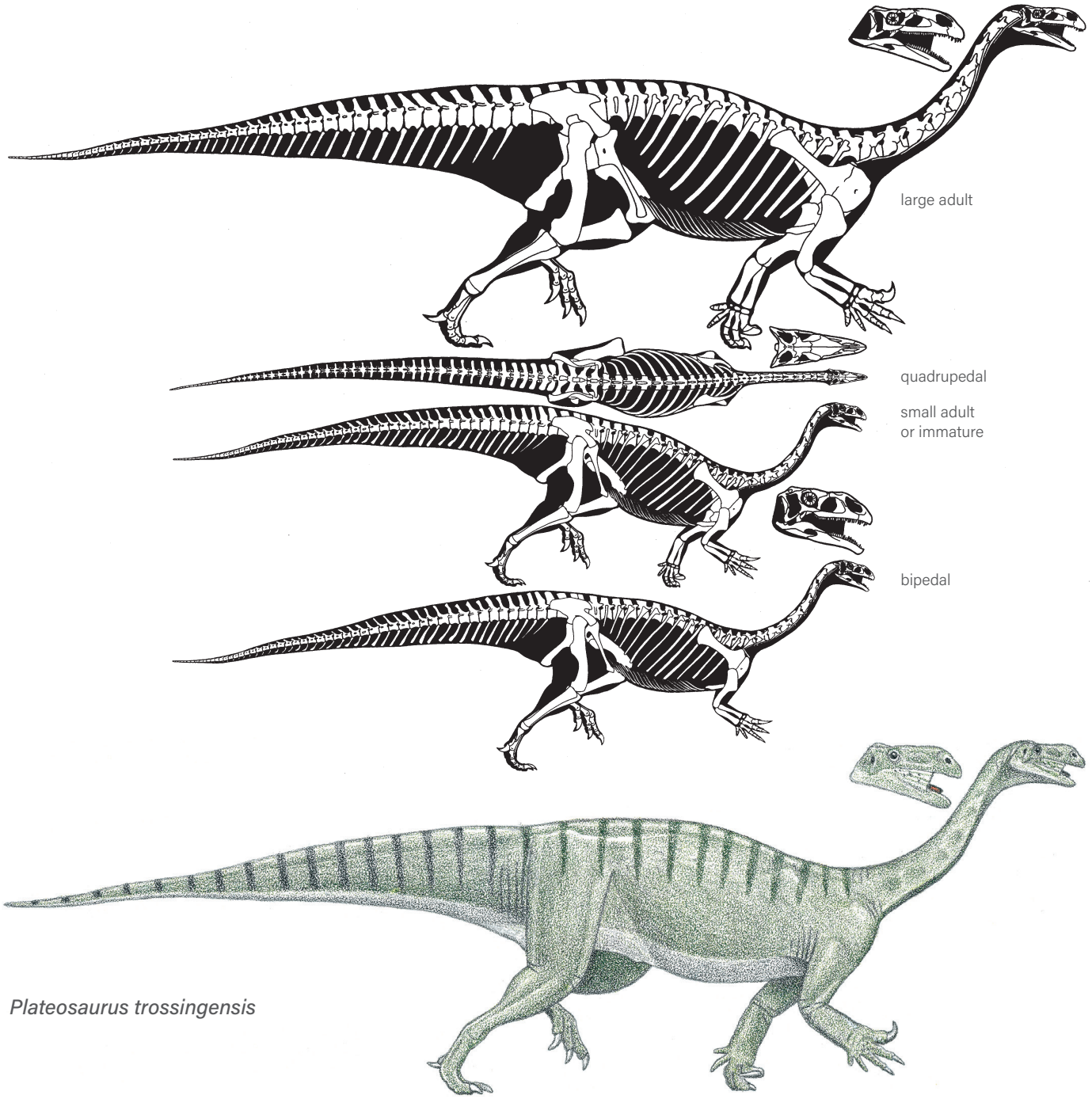
Unaysaurus tolentinoi

Plateosaurus (or *Sellosaurus*) *gracilis*
— 5 m (15 ft) TL, 275 kg (600 lb)
FOSSIL REMAINS Majority of two dozen partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head shallow, subrectangular, snout a little downturned. Arm moderately long. Bi/quadrupedal.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Southern Germany; lower and middle Löwenstein.
NOTES *Efraasia diagnosticus* is probably an immature form of this species. Maximum size uncertain. May be direct ancestor of *P. trossingensis*.

Plateosaurus trossingensis
— 8.5 m (27 ft) TL, 2 tonnes
FOSSIL REMAINS Dozens of complete to partial skulls and skeletons, adult to juvenile, completely known.
ANATOMICAL CHARACTERISTICS Head shallow, narrow, elongated, especially snout, which is a little deeper than back of head, narrow, a little downturned. Skeleton heavily built. Arm moderately long. Bi/quadrupedal.
AGE Late Triassic, late Norian.
DISTRIBUTION AND FORMATION/S Germany, Switzerland, eastern France; Trossingen, Klettgau, Marnes Irisées Supérieures.
ONTOGENY Some individuals fully mature at about half size of other individuals, did not grow through life.
NOTES The classic prosauropod known from abundant remains. New large skulls demonstrate long-snouted shape of adult heads. Probably includes *P. longiceps*, *P.engelhardti*, *P. erienbergensis*, *P. integer*, *P. frassianus*,



Plateosaurus trossingensis



Plateosaurus trossingensis

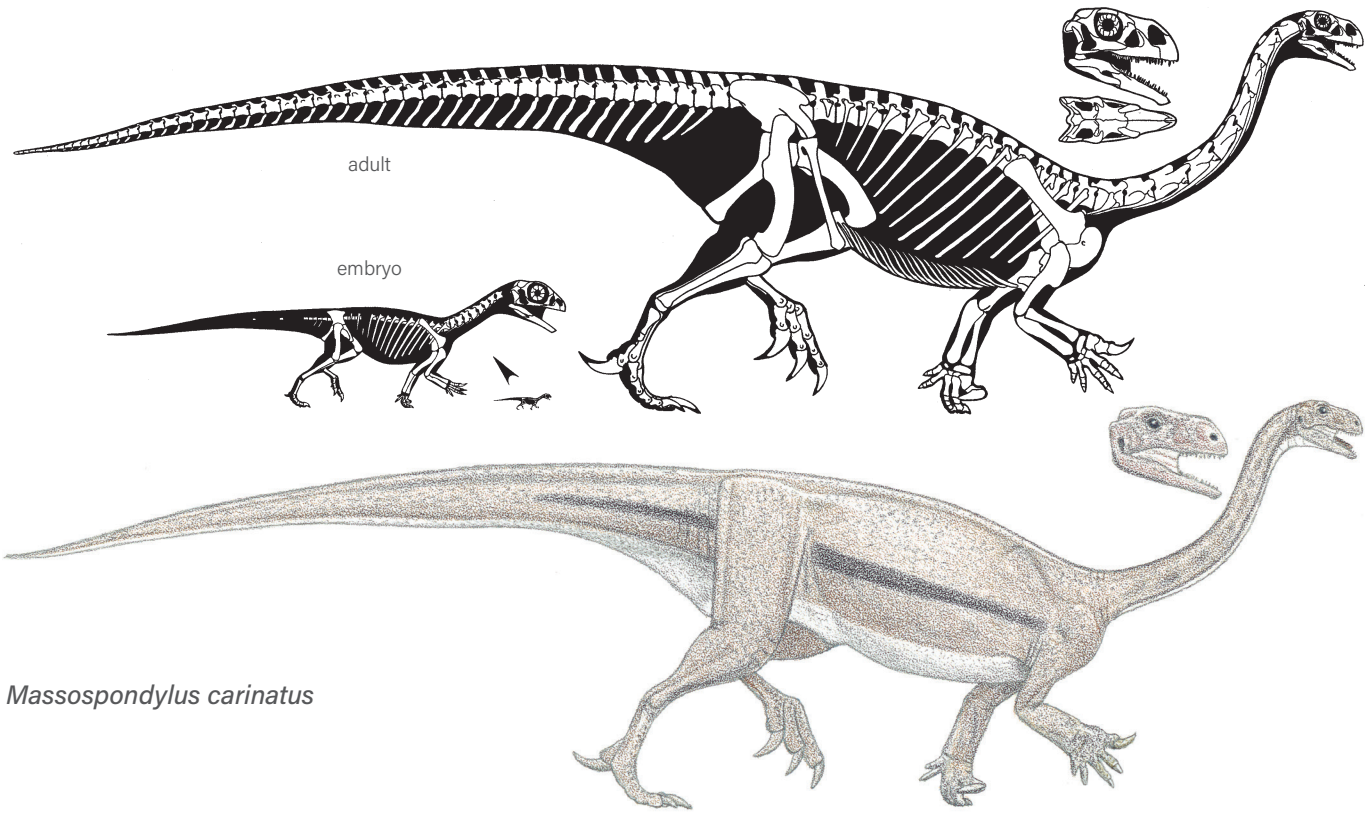
Ruehleia bedheimensis, and *Tuebingosaurus maierfritzorum*; if the latter mature fossil is in this taxon, then indicates *Plateosaurus* is a more derived prosauropod than commonly thought. If larger than *P. gracilis*, may be because of larger predators.

Plateosauravus cullingworthi

— 9 m (30 ft) TL, 2.4 tonnes
FOSSIL REMAINS A few partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa; lower Elliot.
HABITAT/S Arid.
NOTES Was *Euskelosaurus browni*, which is based on inadequate remains.

Kholumolumo ellenbergerorum

— 7 m (23 ft) TL, 1.1 tonne
FOSSIL REMAINS Numerous disarticulated individuals from a bone bed.



Massospondylus carinatus

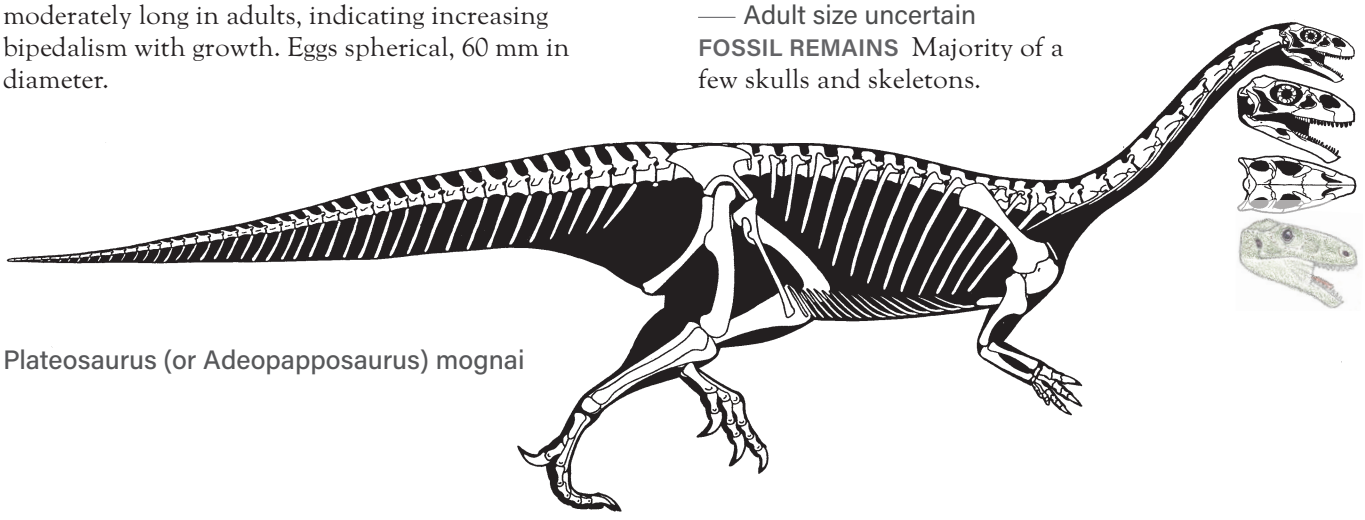
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa; lower Elliot.
HABITAT/S Arid.

Massospondylus carinatus

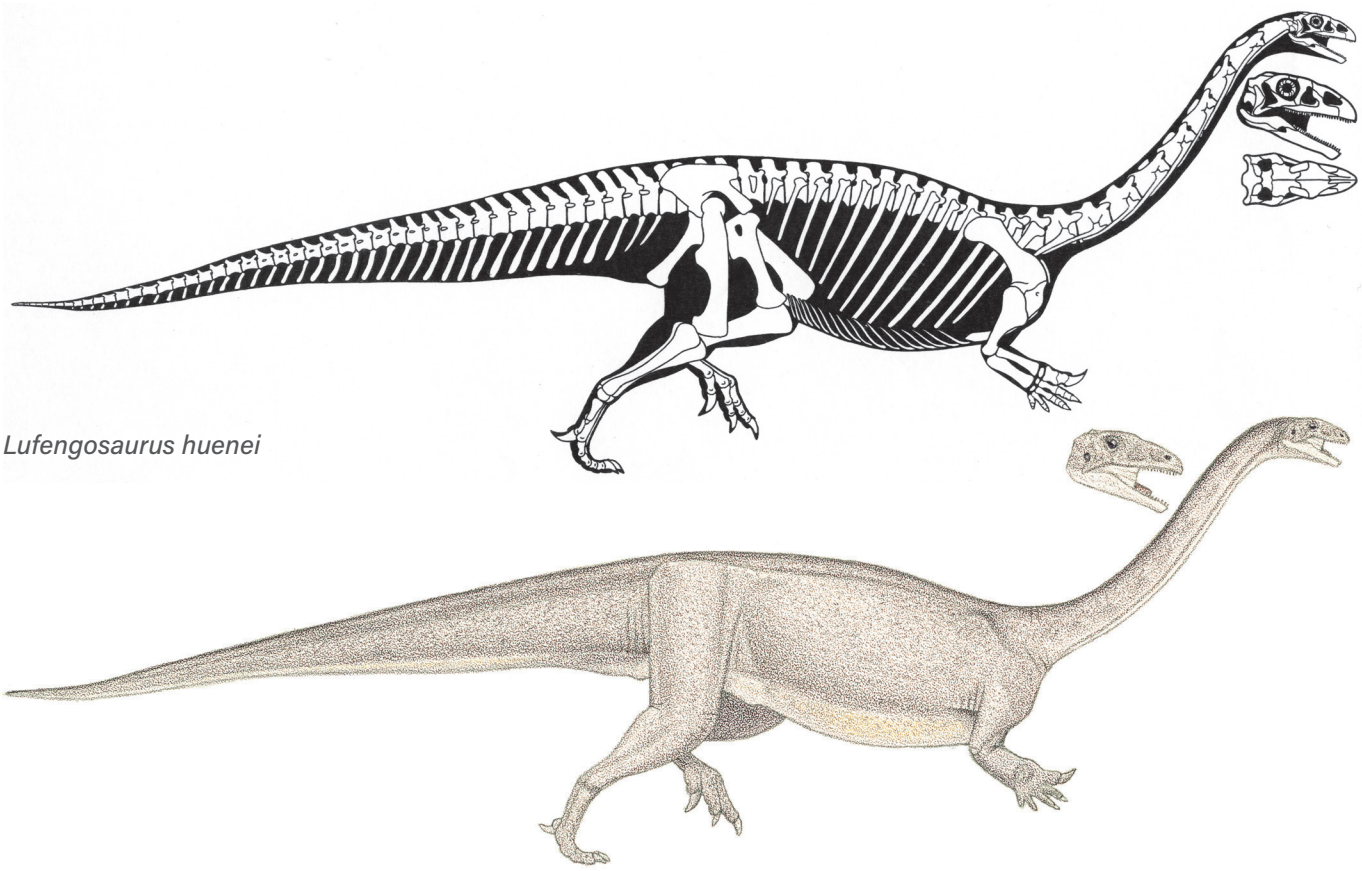
— 4.3 m (14 ft) TL, 195 kg (430 lb)
FOSSIL REMAINS Many dozens of skulls and skeletons, many complete, juveniles to adult, completely known, nests with up to three dozen eggs, embryos.
ANATOMICAL CHARACTERISTICS Head subrectangular. Thumb and foot claws large. Arm long in juveniles, moderately long in adults, indicating increasing bipedalism with growth. Eggs spherical, 60 mm in diameter.
AGE Early Jurassic, late Hettangian to perhaps early Pliensbachian.
DISTRIBUTION AND FORMATION/S South Africa, Lesotho, Zimbabwe; upper Elliot, Bushveld Sandstone, Upper Karoo Sandstone, Forest Sandstone.
HABITAT/S In at least some locations, desert.
HABITS Probably fed on vegetation along watercourses and at oases. Eggs probably buried and abandoned.
NOTES The original fossil is inadequate, and the time span is suspiciously long for a single species. *Massospondylus kaalae* from the upper Elliot Formation may be a distinct species.

Adeopapposaurus mognai

— Adult size uncertain
FOSSIL REMAINS Majority of a few skulls and skeletons.



Plateosaurus (or Adeopapposaurus) mognai



Lufengosaurus huenei

ANATOMICAL CHARACTERISTICS Head shallow, subrectangular, broad. Arm short. Strongly bipedal.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cañón del Colorado.
NOTES Skeletal proportions not entirely certain.

Leyesaurus marayensis

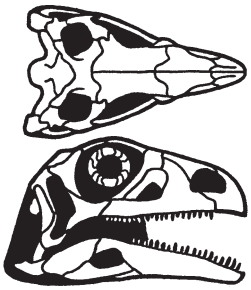
Lufengosaurus huenei
— 9 m (30 ft) TL, 1.7 tonnes
FOSSIL REMAINS Over two dozen skulls and skeletons, some complete, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Neck longer than that of most prosauropods. Arm short. Strongly bipedal.
AGE Early Jurassic, Sinemurian.
DISTRIBUTION AND FORMATION/S Southwestern China; upper Lufeng.
NOTES *L. magnus* probably is adult of this species.

Leyesaurus marayensis
— 3 m (10 ft) TL, 65 kg (140 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head shallow, subrectangular, broad.
AGE Early Jurassic?, Hettangian?
DISTRIBUTION AND FORMATION/S Northwestern Argentina; uppermost Quebrada del Barro.
HABITAT/S Semiarid.

Sarahsaurus aurifontanalis
— 4 m (13 ft) TL, 180 kg (400 lb)
FOSSIL REMAINS Majority of skull and two skeletons.
ANATOMICAL CHARACTERISTICS Head shallow, snout probably a little downturned. Arm short. Strongly bipedal.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Arizona; Kayenta.
HABITAT/S Semiarid.

Coloradisaurus brevis
— 3 m (10 ft) TL, 65 kg (140 lb)
FOSSIL REMAINS Complete skull.
ANATOMICAL CHARACTERISTICS Head short, subtriangular, broad.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Los Colorados.
HABITAT/S Seasonally wet woodlands.

Sarahsaurus aurifontanalis



Coloradisaurus brevis

Xingxiulong chengi

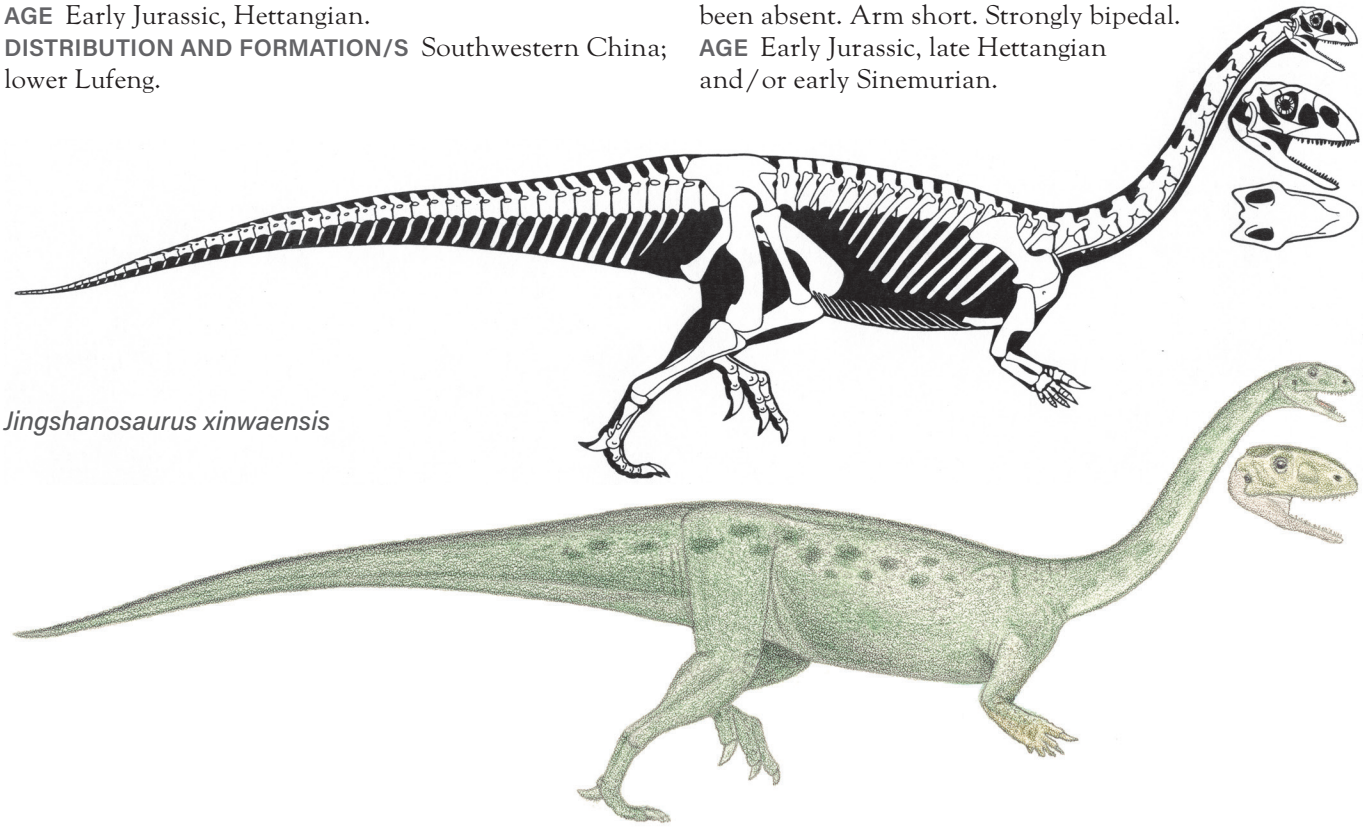
— 6 m (20 ft) TL, 450 kg (1,000 lb)
FOSSIL REMAINS Two partial skulls and majority of skeletons of adult, majority of juvenile skeleton.
ANATOMICAL CHARACTERISTICS Robustly built. Strongly bipedal.
AGE Early Jurassic, Hettangian.
DISTRIBUTION AND FORMATION/S Southwestern China; lower Lufeng.

Chuxiongosaurus lufengensis

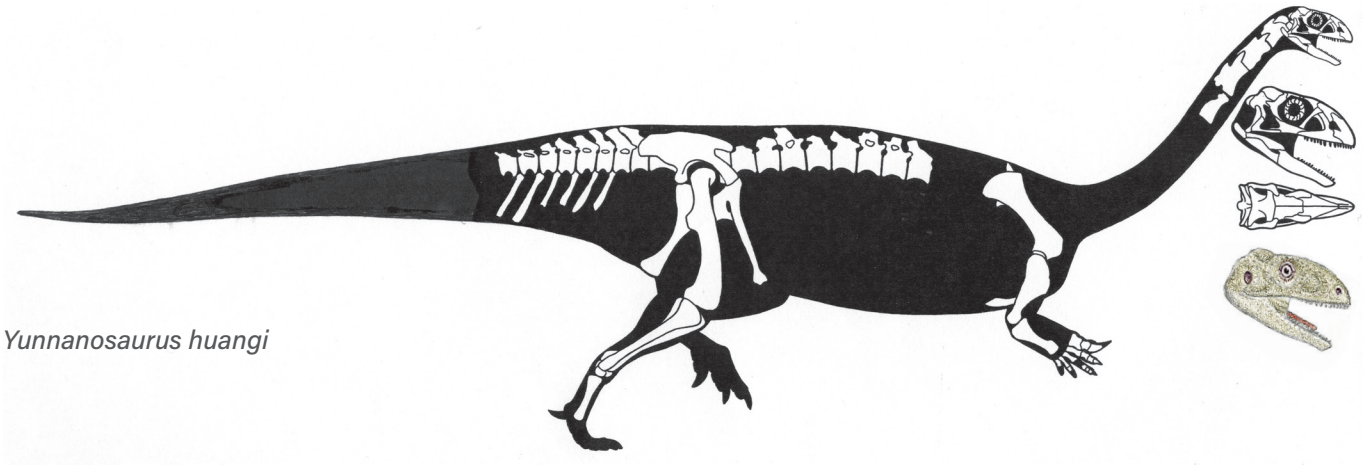
— 4 m (13 ft) TL, 180 kg (400 lb)
FOSSIL REMAINS Nearly complete skull.
ANATOMICAL CHARACTERISTICS Head deep, subtriangular, broad.
AGE Early Jurassic, Hettangian.
DISTRIBUTION AND FORMATION/S Southwestern China; lower Lufeng.

Jingshanosaurus xinwaensis

— 9 m (30 ft) TL, 1.7 tonnes
FOSSIL REMAINS Complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Head subtriangular, broad, cheeks may have been absent. Arm short. Strongly bipedal.
AGE Early Jurassic, late Hettangian and/or early Sinemurian.



Jingshanosaurus xinwaensis



Yunnanosaurus huangi

DISTRIBUTION AND FORMATION/S Southwestern China; upper lower Lufeng.

Yunnanosaurus huangi

— 4.5 m (15 ft) TL, 240 kg (500 lb)
FOSSIL REMAINS Almost two dozen skulls and skeletons, some complete, juvenile to adult.
ANATOMICAL CHARACTERISTICS Head small, subtriangular, cheeks may have been absent. Arm short. Strongly bipedal.
AGE Early Jurassic, Sinemurian.
DISTRIBUTION AND FORMATION/S Southwestern China; upper Lufeng.
NOTES *Y. robustus* is probably the adult of this species.

Yimenosaurus youngi

Yimenosaurus youngi

— 9 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of skull, numerous partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head deep, subrectangular.
AGE Early Jurassic, Pliensbachian.
DISTRIBUTION AND FORMATION/S Southwestern China; upper? Fengjiahe.
NOTES Was thought to be from Middle Jurassic. *Irisosaurus yimenensis* may be an immature example of this species.

Seitaad ruessi

— 3 m (10 ft) TL, 65 kg (140 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Arm moderately short. Predominantly bipedal.
AGE Early Jurassic, Pliensbachian.
DISTRIBUTION AND FORMATION/S Utah; lower Navajo Sandstone.
HABITAT/S Dune desert.

Eucnemesaurus fortis

— 8 m (26 ft) TL, 1.4 tonnes
FOSSIL REMAINS Small portion of a few skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa; lower Elliot.
HABITAT/S Arid.
NOTES The scanty remains were once labeled *Aliwalia rex*, which was thought to be a giant basotheropod. *Eucnemesaurus entaxonis* is probably the adult of this species.

Blikanasaurus cromptoni

— 4 m (13 ft) TL, 200 kg (450 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Leg massively built.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa; lower Elliot.
HABITAT/S Arid.

Mussaurus patagonicus

— 6.5 m (20 ft) TL, 500 kg (1,100 lb)
FOSSIL REMAINS Many dozens of skulls and skeletons from majority to partial, mainly juveniles including embryos and hatchlings up to adults, many dozens of eggs.
ANATOMICAL CHARACTERISTICS Quadrupedal to more bipedal with growth.
AGE Late Triassic, Norian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Laguna Colorada.
HABITS Small juveniles may have supplemented diet with insects.

Mussaurus patagonicus
skulls growth series

NOTES Partial nature of most remains and incomplete description hinder restorations.

Sefapanosaurus zastronensis
— 4 m (9 ft) TL, 200 kg (400 lb)
FOSSIL REMAINS Four partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, Norian.
DISTRIBUTION AND FORMATION/S South Africa; Elliot, level uncertain.
HABITAT/S Arid.

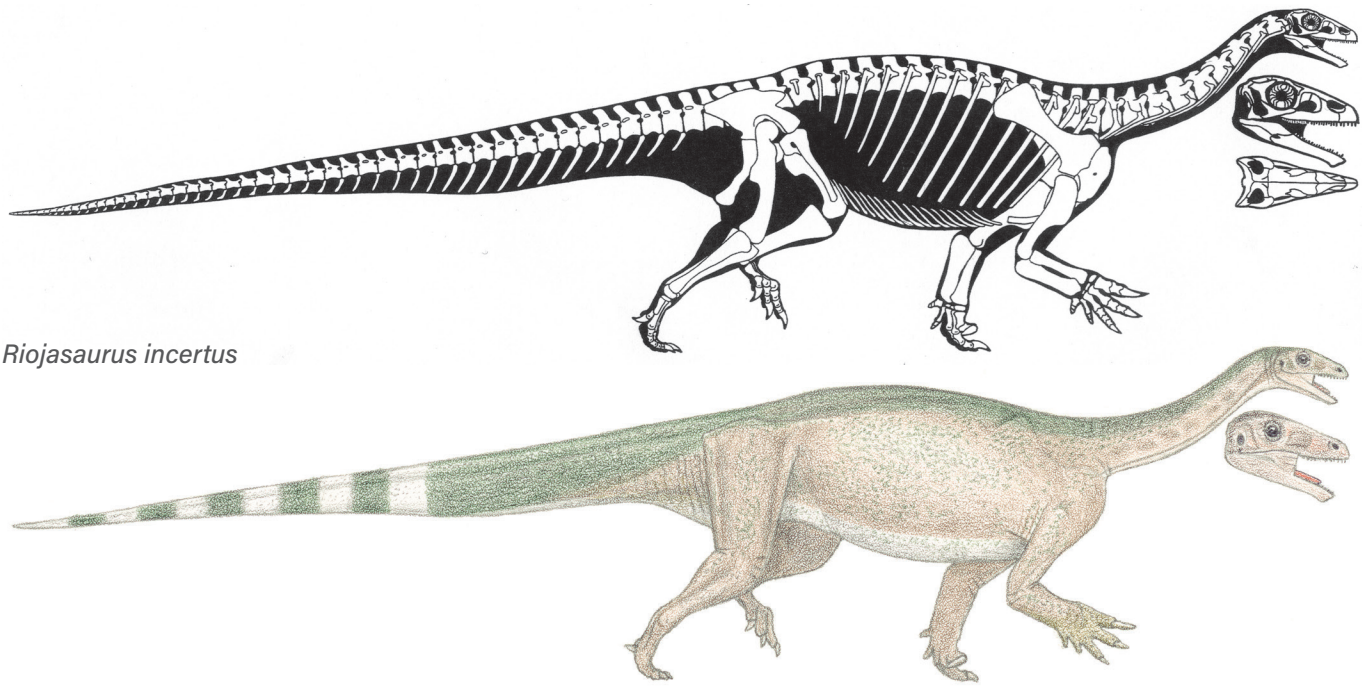
Lessemsaurus sauropoides
— 9 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Los Colorados.
HABITAT/S Seasonally wet woodlands.

Camelotia borealis
— 10 m (33 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S Southwestern England; Westbury.

Aardonyx celestae
— Adult size uncertain
FOSSIL REMAINS Two partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.

Leonerasaurus taquetrensis
— 3 m (10 ft) TL, 70 kg (150 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, late Sinemurian or Pliensbachian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Las Leoneras.

Riojasaurus incertus
— 6.6 m (22 ft) TL, 860 kg (1,900 lb)
FOSSIL REMAINS Complete skull, numerous skeletons of varying completeness, juvenile to adult.
ANATOMICAL CHARACTERISTICS Head subtriangular. Arm long, robust. Strongly quadrupedal.



Riojasaurus incertus

Melanorosaurus readi

AGE Late Triassic, middle Norian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Los Colorados.
HABITAT/S Seasonally wet woodlands.

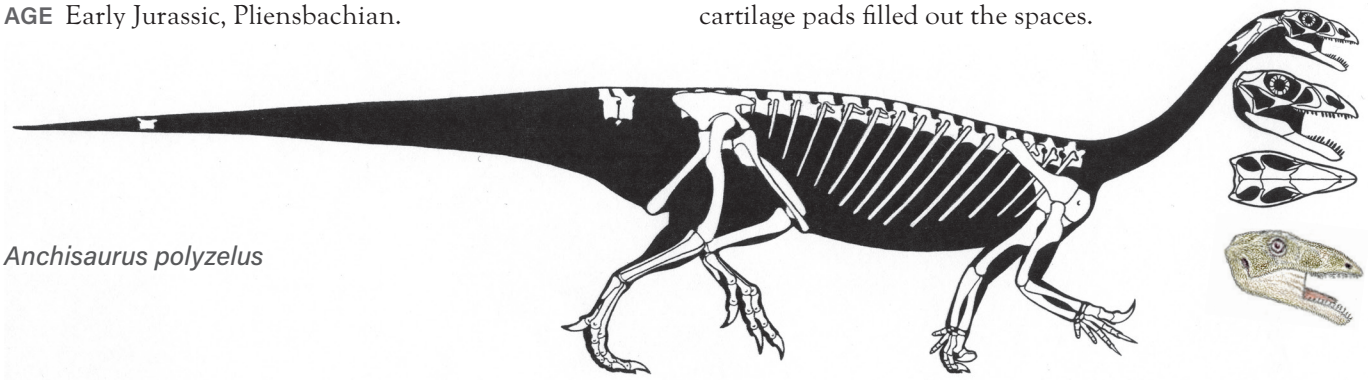
Melanorosaurus readi
— 8 m (26 ft) TL, 1.5 tonnes
FOSSIL REMAINS Complete distorted skull and majority of skeleton, partial remains.
ANATOMICAL CHARACTERISTICS Arm long, robust. Strongly quadrupedal.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa, lower Elliot.
HABITAT/S Arid.

Meroktenos thabanensis
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Robustly built.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa, lower Elliot.
HABITAT/S Arid.
NOTES Was *Melanorosaurus thabanensis*.

Unnamed genus *youngi*
— 13 m (40 ft) TL, 5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, Pliensbachian.
DISTRIBUTION AND FORMATION/S Southwestern China; Fengjiahe.
NOTES Placement in earlier *Yunnanosaurus* highly problematic. Largest known prosauropod.

Anchisaurus polyzelus
— 2.1 m (7 ft) TL, 21 kg (45 lb)
FOSSIL REMAINS Nearly complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head shallow, subtriangular, broad. Arm moderately long. Bi/quadrupedal.
AGE Early Jurassic, Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S Connecticut, Massachusetts; Portland.
HABITAT/S Semiarid rift valley with lakes.
NOTES *Ammosaurus major* is probably the adult of this species.

Yizhousaurus sunae
— 7 m (23 ft) TL, 1.2 tonnes
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head short, deep, broad. Strongly bipedal.
AGE Early Jurassic, Sinemurian.
DISTRIBUTION AND FORMATION/S Southwestern China; upper Lufeng.
NOTES Combines a somewhat sauropod-type skull with prosauropod-grade skeleton. Aft neck and front truck vertebra are so wedge shaped that it is difficult to position them normally, in life thick cartilage pads filled out the spaces.



Anchisaurus polyzelus

Yizhousaurus sunae

Unnamed genus and species

— 4.5 m (18 ft) TL, 250 kg (500 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, Pliensbachian or Toarcian.
DISTRIBUTION AND FORMATION/S Arizona; Navajo Sandstone.
HABITAT/S Dune desert.
HABITS Probably fed on vegetation along watercourses and at oases.
NOTES Has been placed in *Ammosaurus major* and *Massospondylus*, both options highly problematic.

SAUROPODS

LARGE TO ENORMOUS HERBIVOROUS SAUROPODOMORPHS FROM THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Variable. Skulls and teeth more heavily built than those of prosauropods, nostrils at least somewhat retracted. Skeletons heavily built. Necks moderately to extremely long. Tails moderately to extremely long. Skeletons at least incipiently pneumatic, birdlike, some degree of air sac–ventilated respiratory system present. Quadrupedal when moving normally, arms and legs less flexed than in prosauropods. Lower legs shorter than upper, feet short and broad. Could not achieve full run with suspended phase with all feet off ground at same time.
HABITS Highest browsers to have evolved. Preferred tough vegetation, especially conifers. Hard pressed or unable to completely submerge because of pneumatic bodies.
NOTES Lasting 140 million years or more and regularly rivaling great whales in size, the most successful group of large herbivorous animals that has yet evolved. Trackways from Greenland suggest first examples evolved in Early Jurassic. Absence from Antarctica probably reflects lack of sufficient sampling. Never small, known adults always at least close to 2 tonnes, even when island dwellers, probably because columnar limbs and resulting slow top speeds forced large size to deal with predators.

— VULCANODONTS

LARGE TO GIGANTIC SAUROPODS LIMITED TO THE EARLY JURASSIC OF THE EASTERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads short, snouts narrow and rounded. Necks and tails moderately long. Limbs moderately flexed. Arms moderately long, so shoulders about as high as hips. Hands not forming an arcade, fingers not extremely abbreviated. Pelvic ilia shallow, ankles still markedly flexible. Skeletal pneumaticity partly developed, so birdlike respiratory system developing.
HABITS Probably feeding generalists. Probably able to run slowly, main defense standing and fighting with claws.
ENERGETICS Thermophysiology probably intermediate between that of prosauropods and eusauropods.
NOTES This group is a grade splittable into more divisions. Various anatomical features remain poorly understood. If Late Triassic trackways are those of basal-most sauropods, then small-sized examples had appeared by then. Absence from the Western Hemisphere may reflect lack of sufficient sampling.

Antetonitrus ingenipes
— 13 m (43 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Arm prosauropod-like.
AGE Early Jurassic, Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.
NOTES *Ledumahadi mafube* may be adult of this species. If so is earliest known giant dinosaur, higher mass estimates are problematic.

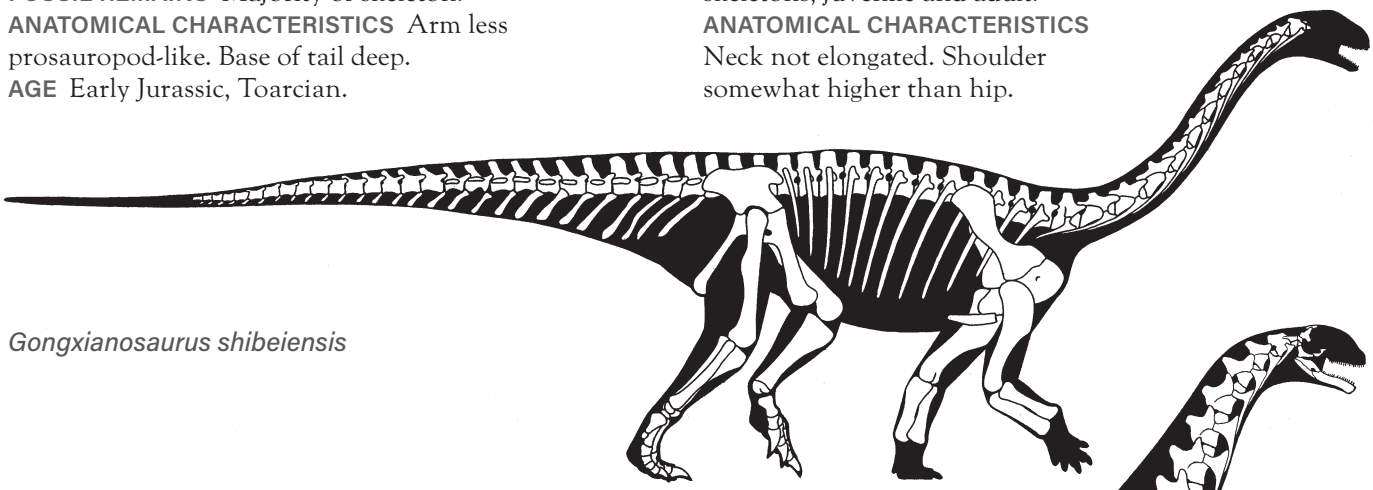
Chinshakiangosaurus chunghoensis
— 10 m (30 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Mouth fairly broad, extensive cheeks present.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Southern China; Fengjiahe.

Gongxianosaurus shibeiensis
— 11 m (35 ft) TL, 3.2 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Arm less prosauropod-like. Base of tail deep.
AGE Early Jurassic, Toarcian.
DISTRIBUTION AND FORMATION/S Central China; Ziliujing.

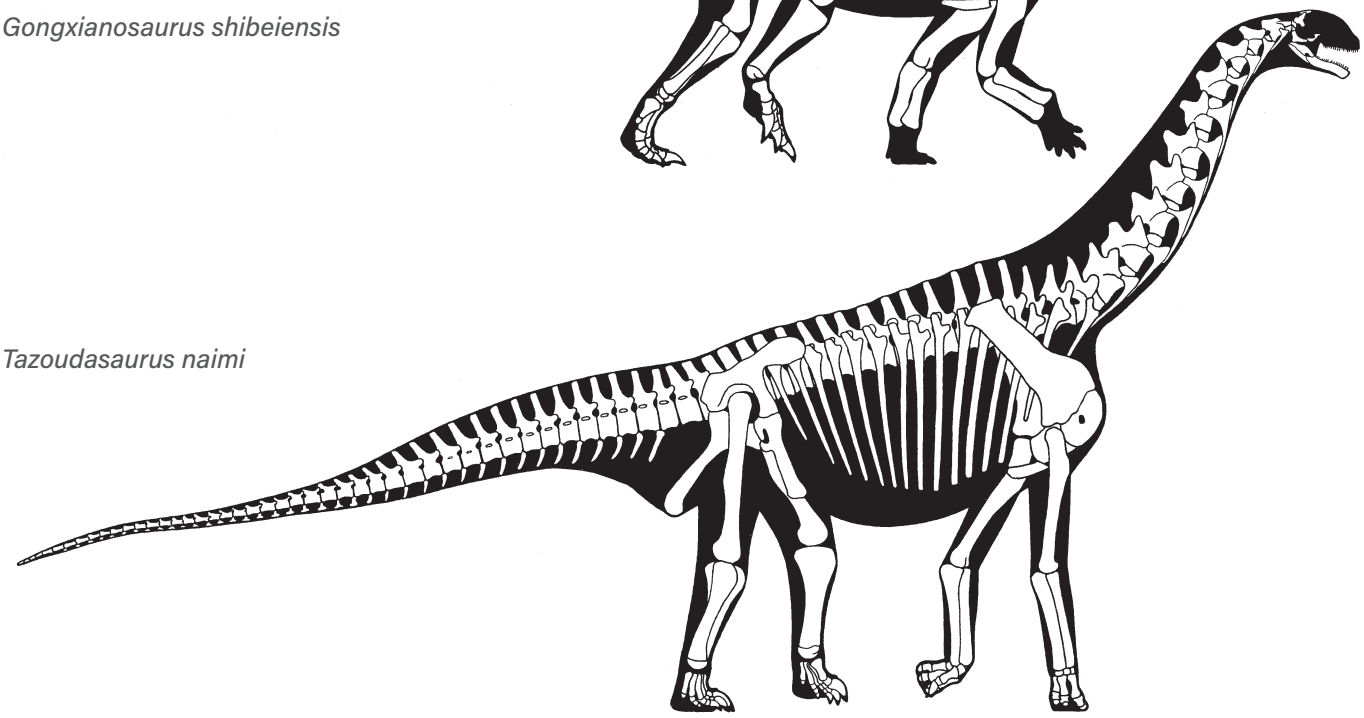
Vulcanodon karibaensis
— 11 m (35 ft) TL, 3.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Jurassic, late Pliensbachian or Toarcian.
DISTRIBUTION AND FORMATION/S Zimbabwe; Batoka.
HABITAT/S Arid.

Pulanesaura eocollum
— 11 m (35 ft) TL, 3.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Jurassic, late Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.

Tazoudasaurus naimi
— 10 m (33 ft) TL, 3.7 tonnes
FOSSIL REMAINS Minority of skull and two skeletons, juvenile and adult.
ANATOMICAL CHARACTERISTICS Neck not elongated. Shoulder somewhat higher than hip.



Gongxianosaurus shibeiensis



Tazoudasaurus naimi

AGE Early Jurassic, Toarcian.
DISTRIBUTION AND FORMATION/S Morocco; Douar of Tazouda.

Kotasaurus yamanpalliensis
— 9 m (30 ft) TL, 2.5 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Southeastern India; Kota.

Isanosaurus attavipachi
— 13 m (43 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of several skeletons, juvenile and adult.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Jurassic.
DISTRIBUTION AND FORMATION/S Thailand; Nam Phong.
NOTES The large remains are probably the adult of the juvenile remains named *Isanosaurus*. Originally incorrectly thought to be from the Late Triassic and thereby showing evolution of giant sauropods soon after first appearance of dinosaurs, instead may be from Late Jurassic.

— EUSAUROPODS

LARGE TO ENORMOUS SAUROPODS FROM THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly variable. Snouts broader, rounded or squared off, nostrils further retracted, cheeks absent. Skeletons massively built. Necks moderately to extremely long. Trunks compact, deep, vertebral series usually stiffened. Tails moderately to extremely long. Shoulder girdles large, hands forming vertical arcades, fingers very short and rigid or lost, no padding, large claws limited to thumbs or lost. Pelves large, ilia deep and strongly arced at top, indicating enlarged upper leg muscles, pubes subvertical, lower legs shorter than upper, mobility of ankles limited, feet very short and broad, five toes short and underlain by large pads, inner toes bearing large claws increasing in size progressing inward. Quadrupedal when moving normally, arms and legs columnar and massively built, so not able to amble faster than elephants. Skeletal pneumaticity and birdlike respiratory system better developed. Skin consisting of small scales often in rosette patterns.
ONTOGENY Growth rates moderate in at least some smaller species to moderately rapid, especially in giants; life spans may have approached and exceeded 100 years.
HABITATS Seasonally dry, open woodlands and prairies, and coastal wetlands, from tropics to polar regions.
HABITS High-level browsers and low-level grazers. Too slow to flee attackers, main defense standing and lashing out with clawed hands and feet or swinging tails, which often weighed tonnes and matched giant attacking theropods in mass. Long, tall necks may have been used for competitive display within species; delicate construction indicates they were not used as impact weapons for combat within species like giraffe necks. Trackways indicate that small juveniles formed pods of similar-sized individuals separate from the herds of large juveniles and adults over 1 tonne. Numerous trackways laid down along watercourses show that many sauropods of all sizes used shorelines to travel, but ability to move into water was limited because the narrow, padless hands were in danger of getting bogged down in soft sediments, as appears to have happened in some fossils. Probably used clawed hind feet to dig for water in streambeds during droughts.
ENERGETICS Power production probably unusually high in longer-necked examples so that powerful heart could pump blood at very high pressures up to high-held brains.
NOTES The dinosaurs most similar to elephants and giraffes. Fragmentary remains and trackways indicate that some eusauropods approached and exceeded 100 tonnes, may have reached 200 tonnes.

— BASO-EUSAUROPODS

LARGE EUSAUROPODS LIMITED TO THE MIDDLE TO LATE JURASSIC.

ANATOMICAL CHARACTERISTICS Heads short, snouts rounded. Necks rather short to moderately long, able to elevate subvertically. Tails moderately long. Arms moderately long, so shoulders as high as hips.
HABITS Low to mid-level browsers.
NOTES Geographic distribution not yet known.

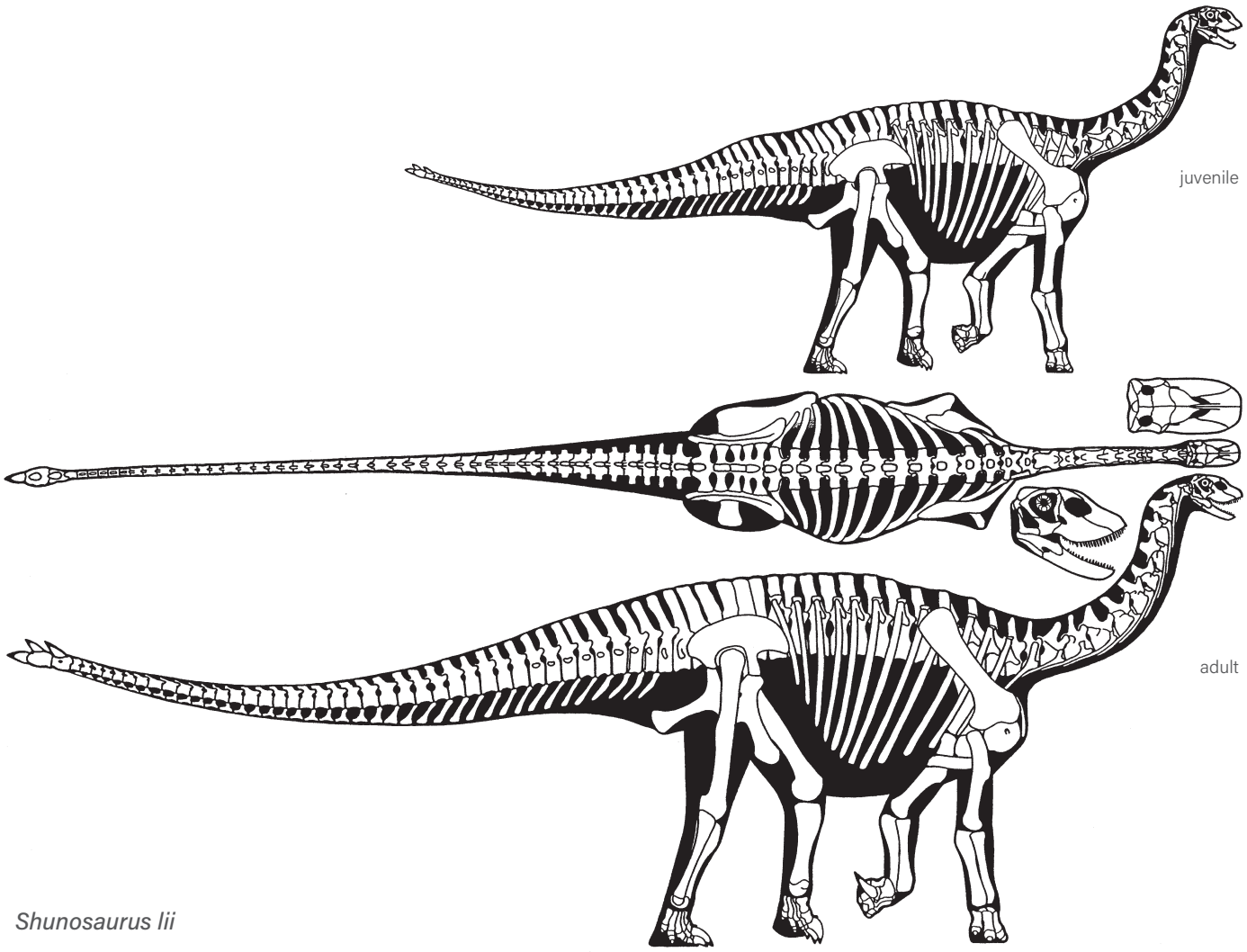
Shunosaurus lii
— 9.5 m (30 ft) TL, 3.3 tonnes
FOSSIL REMAINS Numerous skulls and skeletons, completely known.
ANATOMICAL CHARACTERISTICS Neck short by sauropod standards. Sled-shaped chevrons under tail facilitated static rearing with tail as a prop. Tail tipped by small, spiked club. Arm and especially leg long, shoulders about as high as hips.

Shunosaurus lii and *Gasosaurus constructus*

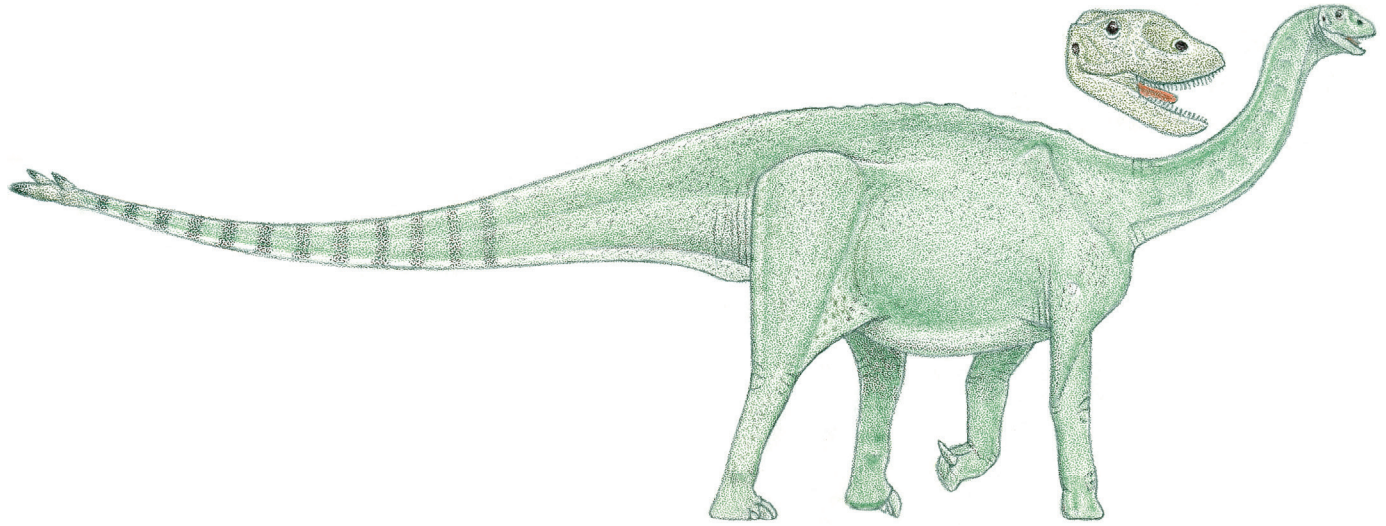
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
HABITS Fed at medium heights. Defense included high-velocity impacts from tail club, which was probably also used in intraspecific combat.
NOTES Almost as short necked as *Brachytrachelopan*.

Unnamed genus? *jiangyiensis*

— 15 m (50 ft) TL, 13 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Leg long.
AGE Middle Jurassic, probably Callovian.
DISTRIBUTION AND FORMATION/S Central China; upper Xiashaximiao.
HABITAT/S Heavily forested.
NOTES Placement in earlier, smaller *Shunosaurus* problematic.



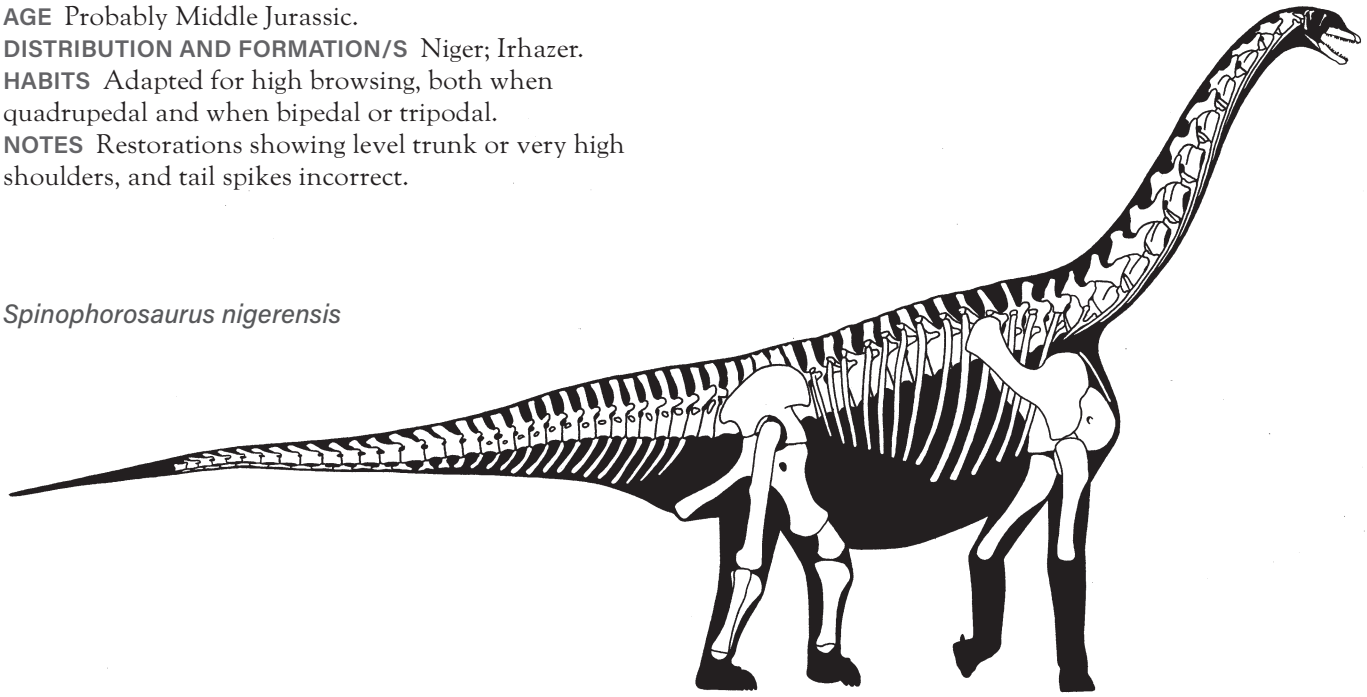
Shunosaurus lii



Spinophorosaurus nigerensis
— 12 m (40 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of skulls, majority of skeletons.

ANATOMICAL CHARACTERISTICS Head small, teeth stout. Neck moderately long. Tail base deep, sled-shaped chevrons under tail facilitated static rearing with tail as a prop. Shoulders appear moderately high.

AGE Probably Middle Jurassic.
DISTRIBUTION AND FORMATION/S Niger; Irhazer.
HABITS Adapted for high browsing, both when quadrupedal and when bipedal or tripodal.
NOTES Restorations showing level trunk or very high shoulders, and tail spikes incorrect.



Spinophorosaurus nigerensis

— CETIOSAURS

LARGE TO GIGANTIC EUSAUROPODS LIMITED TO THE JURASSIC OF THE NORTHERN AND SOUTHERN HEMISPHERES.

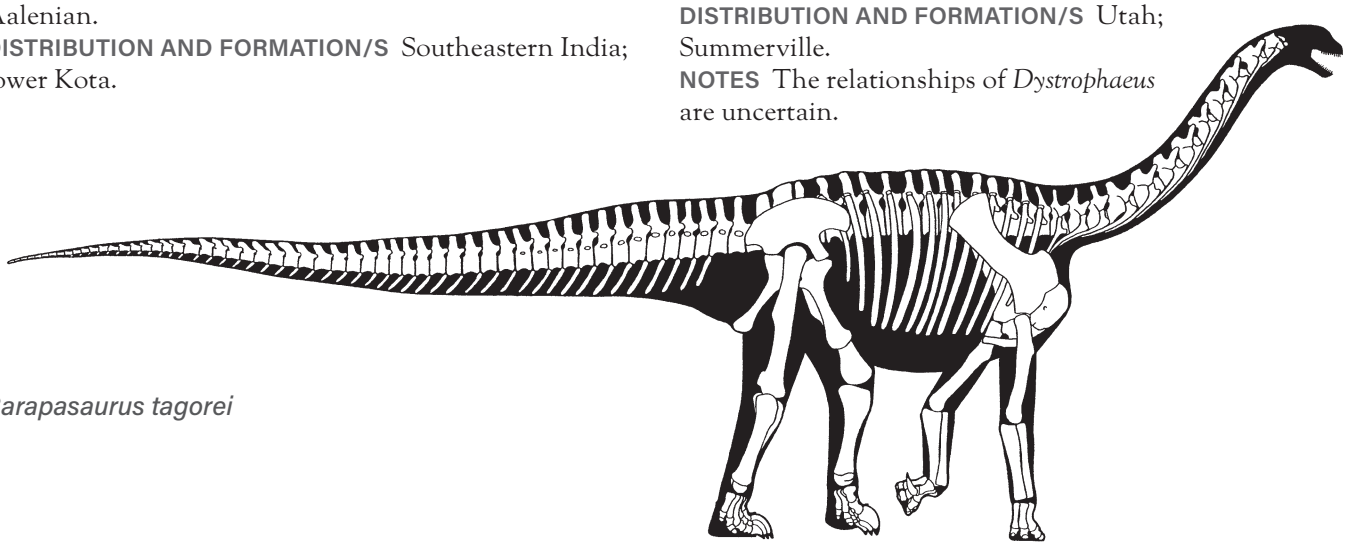
ANATOMICAL CHARACTERISTICS Fairly uniform. Heads short, snouts rounded. Necks moderately long, able to elevate subvertically. Tails moderately long. Arms moderately long, so shoulders about as high as hips.
HABITS Probably feeding generalists.
NOTES Largely a grade of basal eusauropods, the relationships of many of these sauropods are uncertain.

Barapasaurus tagorei

— 12 m (40 ft) TL, 7 tonnes
FOSSIL REMAINS Majority of skeleton from bone beds.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Early or middle Early Jurassic, Toarcian or Aalenian.
DISTRIBUTION AND FORMATION/S Southeastern India; lower Kota.

Dystrophaeus viaemalae

— 13 m (43 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle and/or Late Jurassic, Callovian and/or Oxfordian.
DISTRIBUTION AND FORMATION/S Utah; Summerville.
NOTES The relationships of *Dystrophaeus* are uncertain.



Barapasaurus tagorei

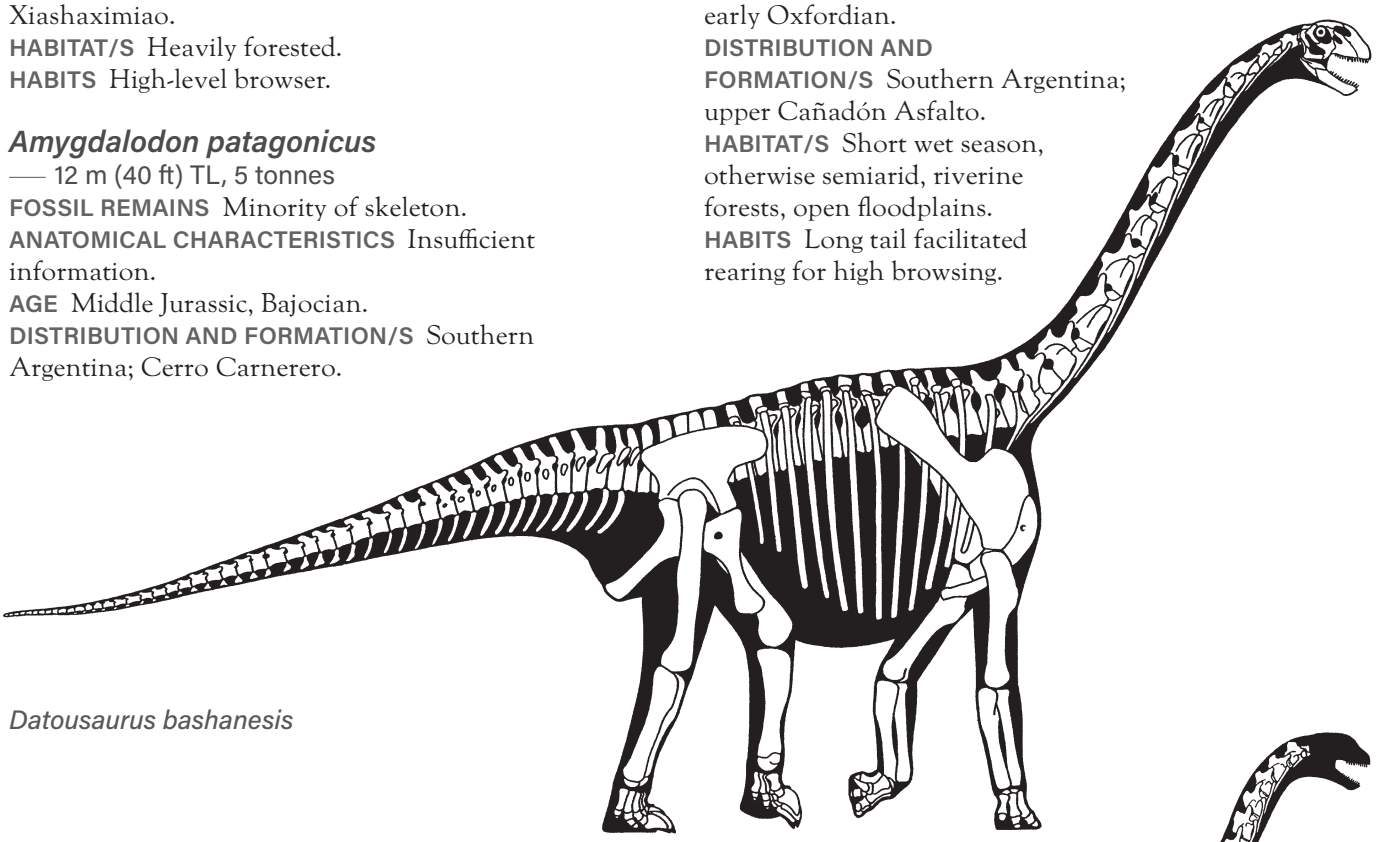
Rhoetosaurus brownei
— 15 m (50 ft) TL, 9 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Bajocian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; Hutton.
HABITAT/S Polar forests with warm, daylight-dominated summers and cold, dark winters.

Datousaurus bashanensis
— 10 m (34 ft) TL, 4.7 tonnes
FOSSIL REMAINS Partial skull and skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long. Shoulder a little higher than hip.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
HABITS High-level browser.

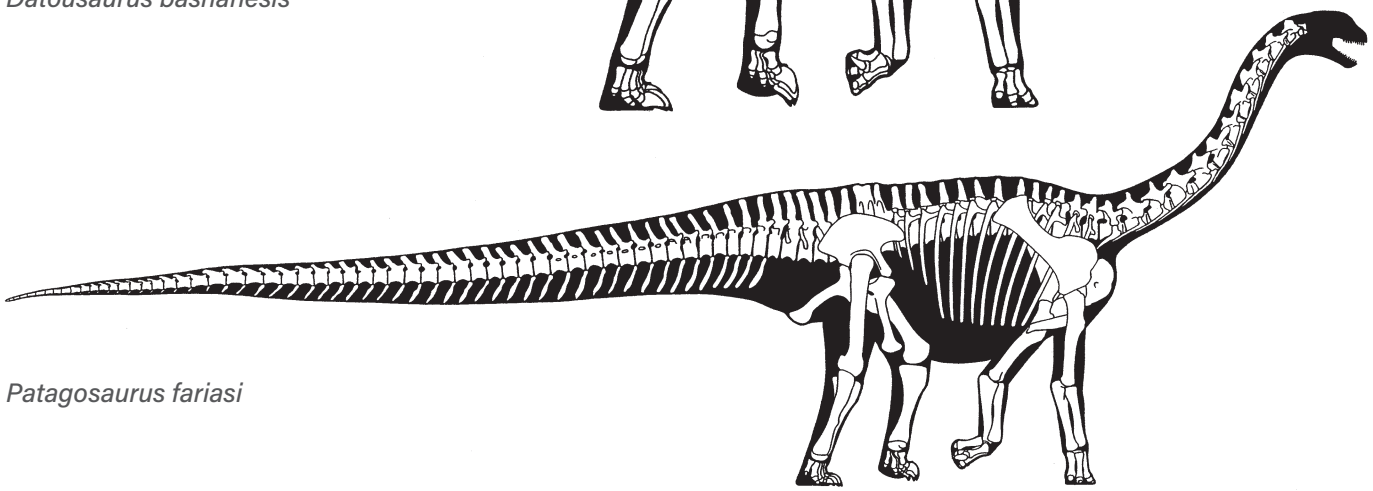
Amygdalodon patagonicus
— 12 m (40 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Bajocian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cerro Carnerero.

Bagualia alba
— 12 m (40 ft) TL, 4 tonnes
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Early Jurassic, early middle Toarcian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Cañadón Asfalto.
HABITAT/S Short wet season, otherwise semiarid, riverine forests, open floodplains.

Patagosaurus fariasi
— 16.5 m (53 ft) TL, 9.3 tonnes
FOSSIL REMAINS Minority of skull and numerous skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long. Tail long.
AGE Middle or Late Jurassic, late Callovian and/or early Oxfordian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Cañadón Asfalto.
HABITAT/S Short wet season, otherwise semiarid, riverine forests, open floodplains.
HABITS Long tail facilitated rearing for high browsing.



Datousaurus bashanesis



Patagosaurus fariasi

Volkheimeria chubutensis
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, middle Toarcian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Cañadón Asfalto.

Chebsaurus algeriensis
— Adult size uncertain
FOSSIL REMAINS Two partial skeletons, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, probably Callovian.
DISTRIBUTION AND FORMATION/S Algeria; unnamed.

Ferganasaurus verzilini
— 18 m (60 ft) TL, 15 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Callovian.
DISTRIBUTION AND FORMATION/S Kyrgyzstan; Balabansai.
NOTES The claim that there are two hand claws is problematic.

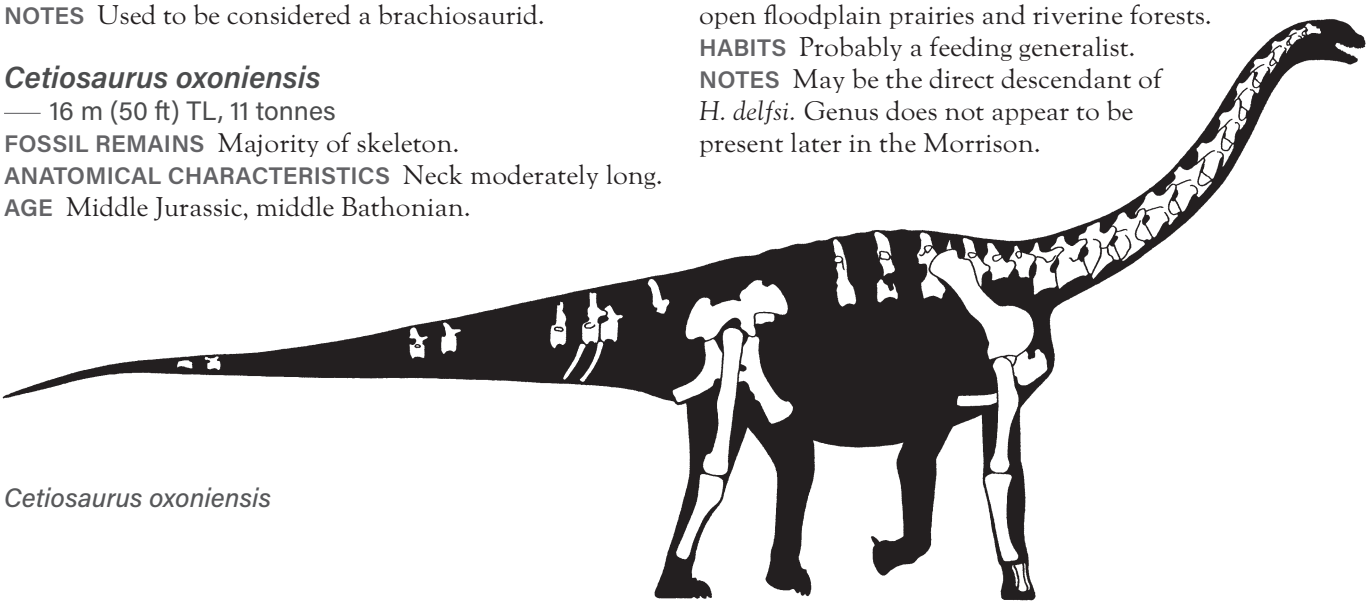
Lapparentosaurus madagascariensis
— Adult size uncertain
FOSSIL REMAINS A few partial skeletons, subadult to juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Bathonian.
DISTRIBUTION AND FORMATION/S Madagascar; Sakahara.
NOTES Used to be considered a brachiosaurid.

Cetiosaurus oxoniensis
— 16 m (50 ft) TL, 11 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Middle Jurassic, middle Bathonian.
DISTRIBUTION AND FORMATION/S Central England; Forest Marble.
NOTES First known sauropod.

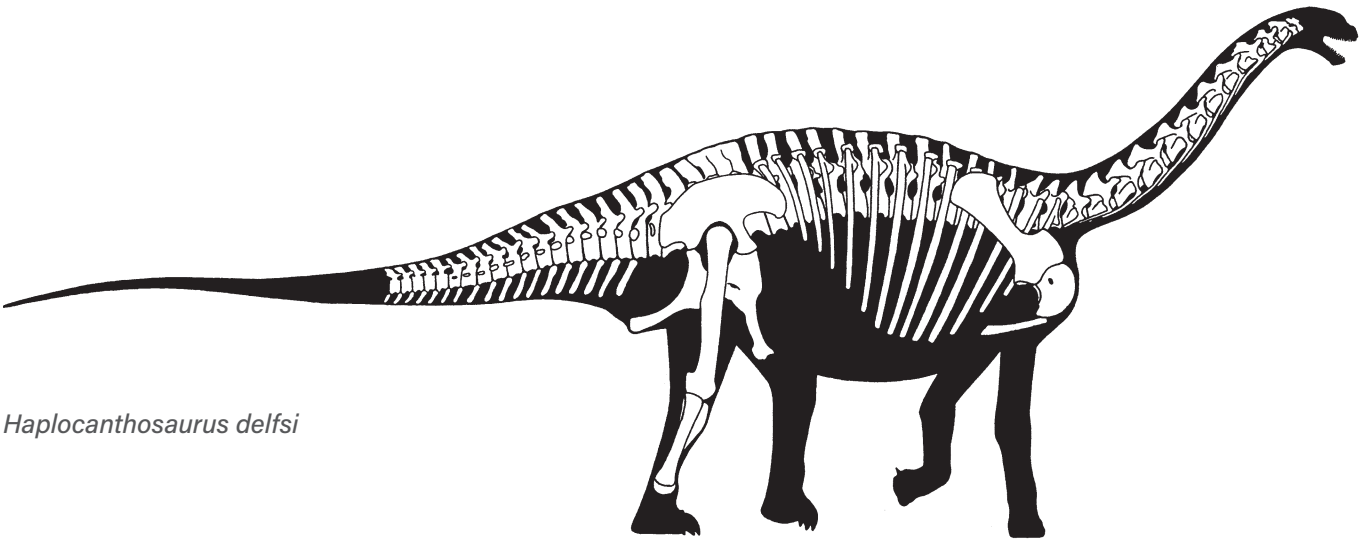
Cetiosauriscus stewarti
— 15 m (50 ft) TL, 10 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Callovian.
DISTRIBUTION AND FORMATION/S Eastern England; lower Oxford Clay.
NOTES Not a diplodocoid as was suggested.

Haplocanthosaurus delfsi
— 16 m (55 ft) TL, 14.4 tonnes
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Colorado; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Probably a feeding generalist.
NOTES Whether this is a different species from the slightly later *H. priscus* is uncertain. *Haplocanthosaurus* may have been a basal diplodocoid.

Haplocanthosaurus priscus
— 12 m (40 ft) TL, 5.6 tonnes
FOSSIL REMAINS Majority of two skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Probably a feeding generalist.
NOTES May be the direct descendant of *H. delfsi*. Genus does not appear to be present later in the Morrison.



Cetiosaurus oxoniensis

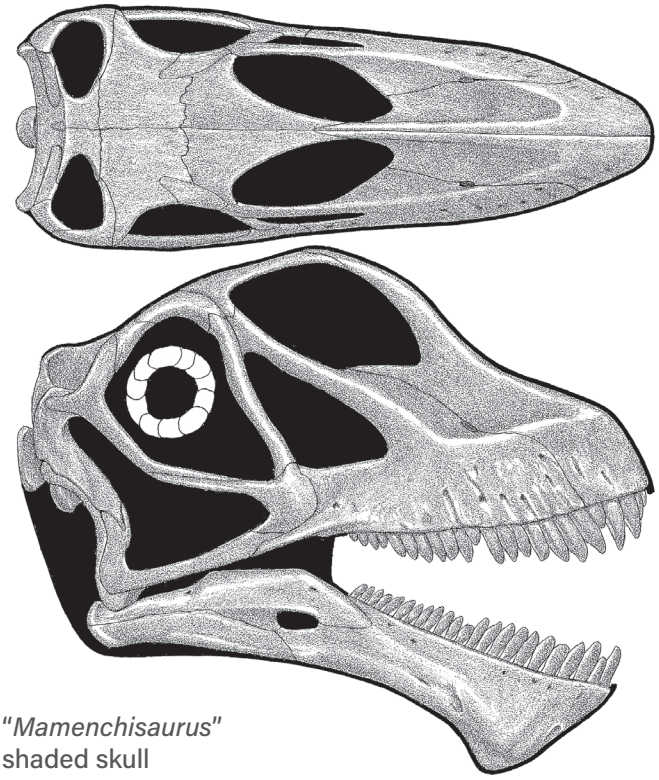


Haplocanthosaurus delfsi

— MAMENCHISAURS

LARGE TO GIGANTIC EUSAUROPODS LIMITED TO THE MIDDLE AND LATE JURASSIC OF ASIA.

ANATOMICAL CHARACTERISTICS Variable. Heads short, snouts rounded. Necks long to extremely long, able to elevate vertically. Tails moderately long. Arms long so shoulders somewhat higher than hips, retroverted pelves facilitated slow walking when rearing up by keeping hips and tails horizontal when bipedal, sled-shaped chevrons under tails facilitated static rearing with tails as a prop.
HABITS High-level browsers, both when quadrupedal and when bipedal or tripodal.
NOTES Representing an apparent radiation of Asian sauropods when the continent was isolated; the relationships of these taxa are obscure, with generic designations often problematic; group probably splittable into a number of divisions. Very incomplete, Late Jurassic East African *Wamweracaudia keranje* may be a non-Asian member of this group, which may have survived into very Early Cretaceous.



"*Mamenchisaurus*"
shaded skull

Tonganosaurus hei
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck long.
AGE Early Jurassic.
DISTRIBUTION AND FORMATION/S Southern China; Yimin.
NOTES Whether this early, 12 m long fossil is a mamenchisaur is uncertain.

Chuanjiesaurus anaensis
— 17 m (55 ft) TL, 11 tonnes
FOSSIL REMAINS Two partial skeletons.
ANATOMICAL CHARACTERISTICS Neck very long. Shoulders a little higher than hips. Tail not large.
AGE Middle Jurassic, Bajocian.
DISTRIBUTION AND FORMATION/S Southwestern China; lower Chuanjie.
NOTES One skeleton may be gender of this species, or *C.* (or *Analong*) *chuanjieensis*.

Omeisaurus junghsiensis
— 14 m (45 ft) TL, 4 tonnes
FOSSIL REMAINS Partial skull and skeletons.
ANATOMICAL CHARACTERISTICS Neck very long.
AGE Middle Jurassic, probably Bathonian.

Unnamed genus
tianfuensis

DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.

Unnamed genus *tianfuensis*

— 18 m (60 ft) TL, 9.3 tonnes
FOSSIL REMAINS Majority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Neck extremely long and slender.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
NOTES Too different to be placed in *Omeisaurus*. Claims that this sauropod had a tail club problematic.

Unnamed genus *jiaoi*

— 19 m (62 ft) TL, 12 tonnes
FOSSIL REMAINS Majority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, probably Bathonian.

Unnamed genus *tianfuensis*

DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
NOTES Too different to be placed in *Omeisaurus* or unnamed genus *tianfuensis*.

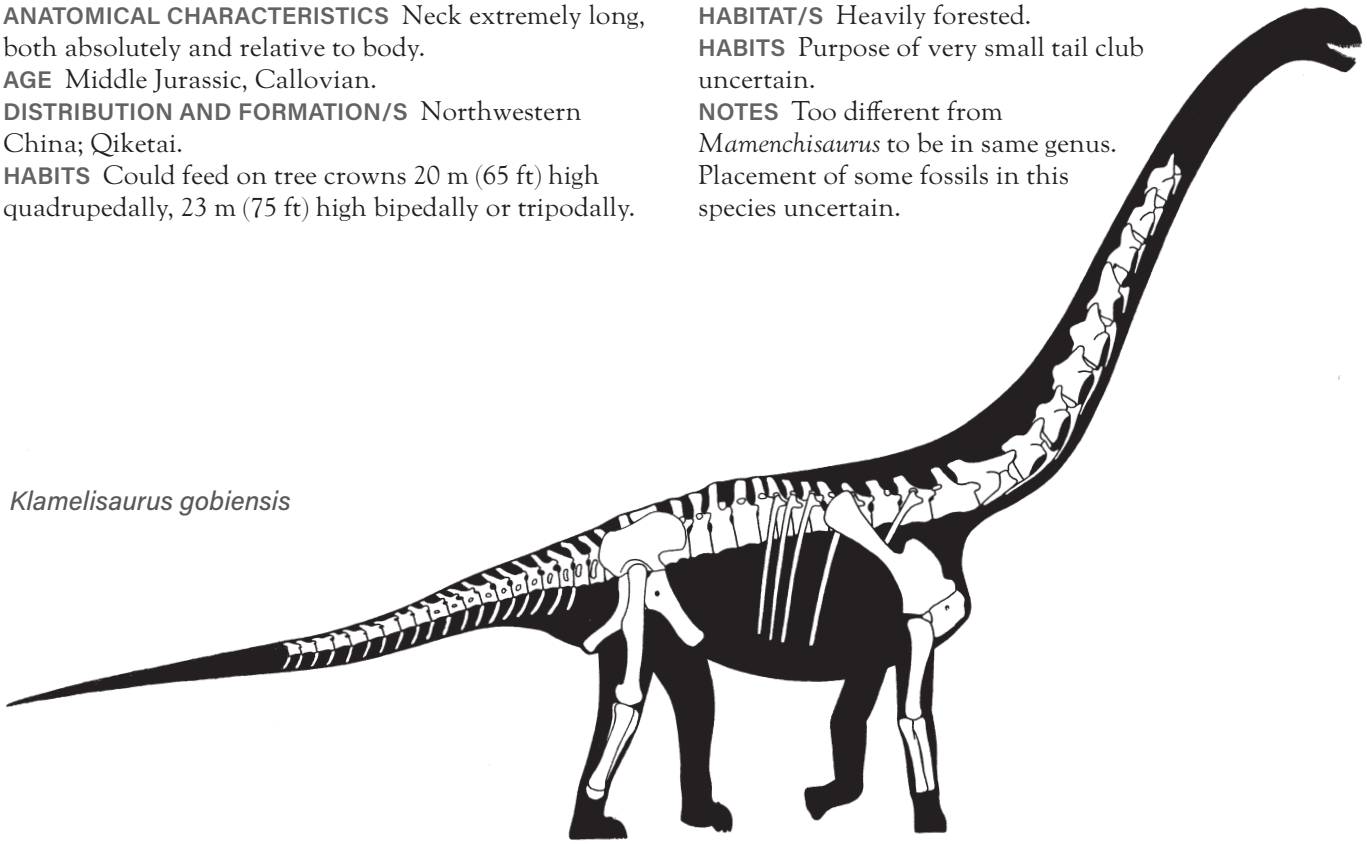
Klamelisaurus gobiensis
— 13 m (45 ft) TL, 8.2 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck long. Shoulders a little higher than hips. Tail not large.
AGE Middle Jurassic, late Callovian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Shishugou.

Yuanmousaurus jiangyiensis
— 17 m (60 ft) TL, 12 tonnes
FOSSIL REMAINS Partial skeleton(s).
ANATOMICAL CHARACTERISTICS
Neck long.
AGE Middle Jurassic.
DISTRIBUTION AND FORMATION/S Southern China; Zhanghe.
NOTES *Eomamenchisaurus yuanmouensis* may be a juvenile of this species.

Xinjiangtitan shanshanesis
— 34 m (110 ft) TL, 40 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck extremely long, both absolutely and relative to body.
AGE Middle Jurassic, Callovian.
DISTRIBUTION AND FORMATION/S Northwestern China; Qiketai.
HABITS Could feed on tree crowns 20 m (65 ft) high quadrupedally, 23 m (75 ft) high bipedally or tripodally.
NOTES Earliest known gigantic sauropod, dinosaur, and land animal. Neck longest known especially based on a complete vertebral series.

Unnamed genus *sinocanadorum*
— Adult size uncertain
FOSSIL REMAINS Minority of skull and minority of skeleton(s).
ANATOMICAL CHARACTERISTICS Neck extremely long.
AGE Late Jurassic, middle and/or late Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.
HABITS Could feed on tree crowns 20 m (65 ft) high quadrupedally, 23 m (75 ft) high bipedally or tripodally.
NOTES A pair of neck vertebrae that may belong to this species are about as long as those of *Xinjiangtitan*, may indicate an individual of same size, or up to ~90 tonnes if proportions were similar to unnamed genus *hochuanensis*, in which case is one of largest known land animals.

Unnamed genus *hochuanensis*
— 21 m (70 ft) TL, 15.5 tonnes
FOSSIL REMAINS Partial skull and a few skeletons.
ANATOMICAL CHARACTERISTICS Neck extremely long, vertebral spines near base of neck forked. Small tail club present. Limbs short.
AGE Late Jurassic, probably Oxfordian.
DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.
HABITAT/S Heavily forested.
HABITS Purpose of very small tail club uncertain.
NOTES Too different from *Mamenchisaurus* to be in same genus. Placement of some fossils in this species uncertain.



Klamelisaurus gobiensis

Unnamed genus *youngi*?

— 17 m (55 ft) TL, 7.7 tonnes

FOSSIL REMAINS Complete skull and majority of skeleton.

ANATOMICAL CHARACTERISTICS Neck extremely long, vertebral spines near base of neck forked. Hip strongly retroverted, and tail directed strongly upward. Limbs short.

AGE Late Jurassic, probably Oxfordian.

DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.

HABITAT/S Heavily forested.

NOTES Among the most peculiarly shaped sauropods. May be a gender of unnamed genus *hochuanensis*.

Mamenchisaurus constructus

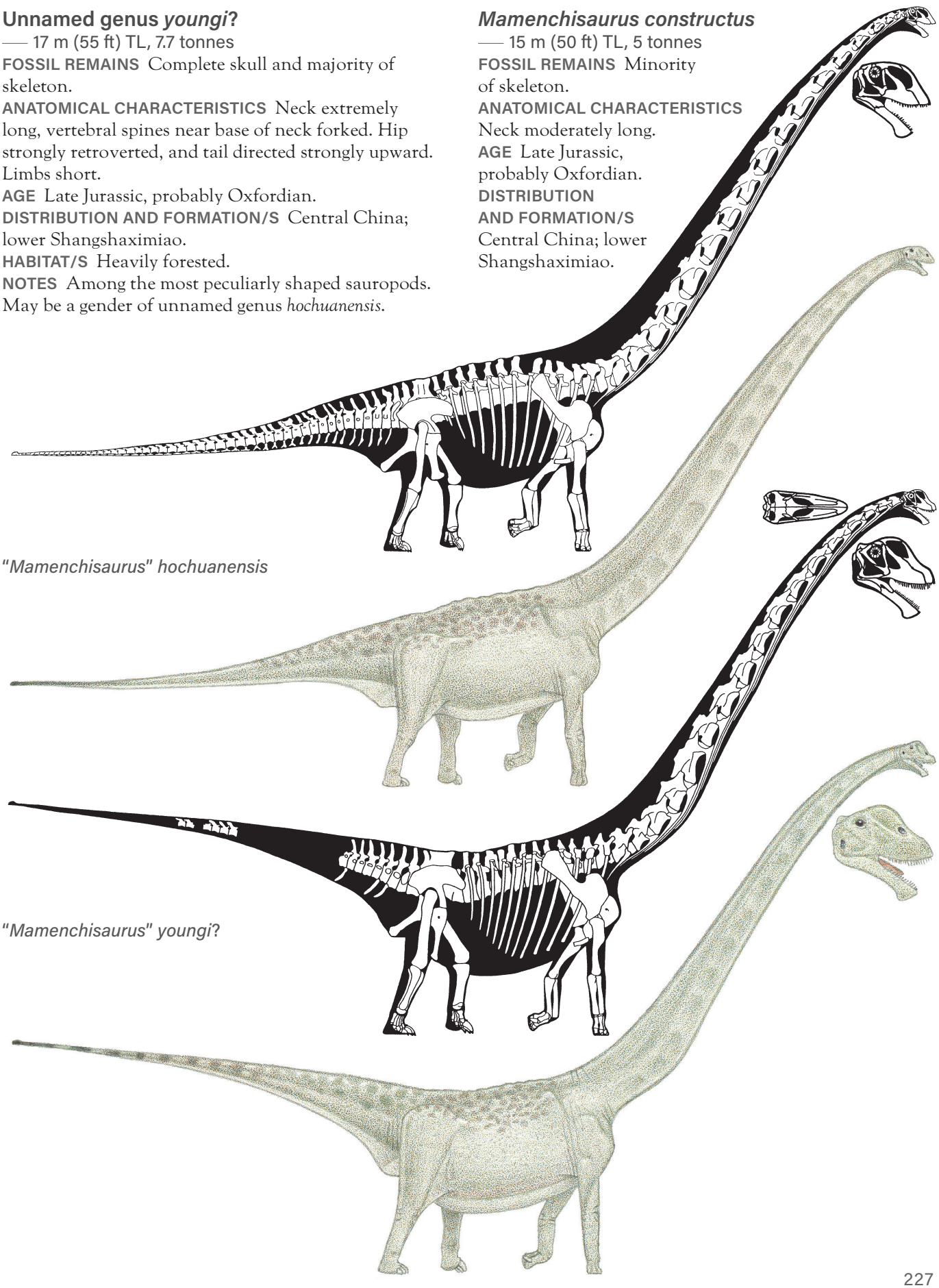
— 15 m (50 ft) TL, 5 tonnes

FOSSIL REMAINS Minority of skeleton.

ANATOMICAL CHARACTERISTICS Neck moderately long.

AGE Late Jurassic, probably Oxfordian.

DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.



"Mamenchisaurus" hochuanensis

"Mamenchisaurus" youngi?

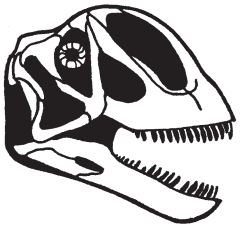
HABITAT/S Heavily forested.
NOTES Based on an inadequate fossil without a very long neck; that so many species have been placed in *Mamenchisaurus*, many from the same formation, indicates that these sauropods are overlumped, being in the wrong genus in some cases, or split into too many species in others.

Unnamed genus *maoianus*
— 15 m (50 ft) TL, 5 tonnes
FOSSIL REMAINS Nearly complete skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Neck very long.
AGE Late Jurassic, probably Oxfordian.
DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.
HABITAT/S Heavily forested.

Uncertain genus *jingyanensis*?
— 20 m (65 ft) TL, 13 tonnes
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck extremely long.
AGE Late Jurassic, probably Oxfordian.
DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.
HABITAT/S Heavily forested.
NOTES Probably belongs to one of the other incomplete species from the lower Shangshaximiao, possibly *Mamenchisaurus*.

Qijianglong guokr
— Adult size uncertain
FOSSIL REMAINS Partial skeleton, probably large juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Central China; Suining.

Unnamed genus *anyuensis*
— 25 m (80 ft) TL, 25 tonnes
FOSSIL REMAINS Several partial skeletons.
ANATOMICAL CHARACTERISTICS Neck extremely long.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Central China; Suining.
NOTES Cannot be in much earlier *Mamenchisaurus*, indicates group survived well into Cretaceous.



unnamed genus *maoianus*

uncertain genus *jingyanensis*?

— TURIASAURS

MEDIUM-SIZED TO ENORMOUS SAUROPODS LIMITED TO THE LATE JURASSIC OF EUROPE.

ANATOMICAL CHARACTERISTICS Necks and tails moderately long. Arms moderately long, so shoulders about as high as hips.

Amanzia greppini
— 10 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Partial remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, early Kimmeridgian.
DISTRIBUTION AND FORMATION/S Switzerland; lower Reuchenette.

Turiasaurus riodevensis
— 30 m (100 ft) TL, 50 tonnes
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Some neck and trunk vertebral spines forked.
AGE Late Jurassic and/or early Cretaceous, late Tithonian and/or earliest Berriasian.
DISTRIBUTION AND FORMATION/S Eastern Spain; Villar del Arzobispo.
NOTES The largest known nonneosauropod.

Losillasaurus giganteus
— Adult size uncertain
FOSSIL REMAINS Minority of several skeletons.
ANATOMICAL CHARACTERISTICS Vertebral spines not forked.
AGE Late Jurassic and/or early Cretaceous, late Tithonian and/or earliest Berriasian.
DISTRIBUTION AND FORMATION/S Eastern Spain; upper Villar del Arzobispo.
NOTES Subadult remains indicate a very large sauropod.

Mierasaurus bobyoungi
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton, other remains of varying ages.
ANATOMICAL CHARACTERISTICS Vertebral spines not forked.
AGE Early Cretaceous, late Berriasian.
DISTRIBUTION AND FORMATION/S Utah; lowermost Cedar Mountain.

Moabosaurus utahensis
— Adult size uncertain
FOSSIL REMAINS Disarticulated bone bed remains of varying ages.
ANATOMICAL CHARACTERISTICS Vertebral spines not forked.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.

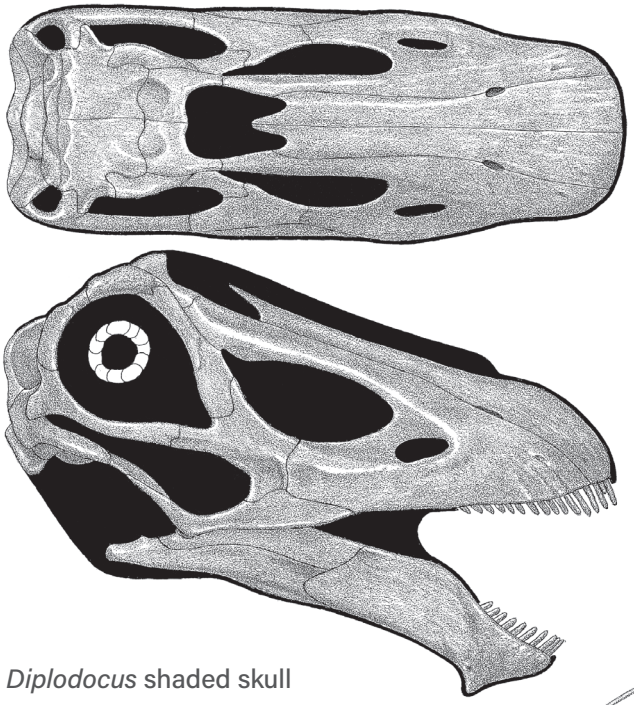
— NEOSAUROPODS

LARGE TO ENORMOUS EUSAUROPODS OF THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Skeletal pneumaticity and birdlike respiratory system well developed.
NOTES Absence from Antarctica probably reflects lack of sufficient sampling.

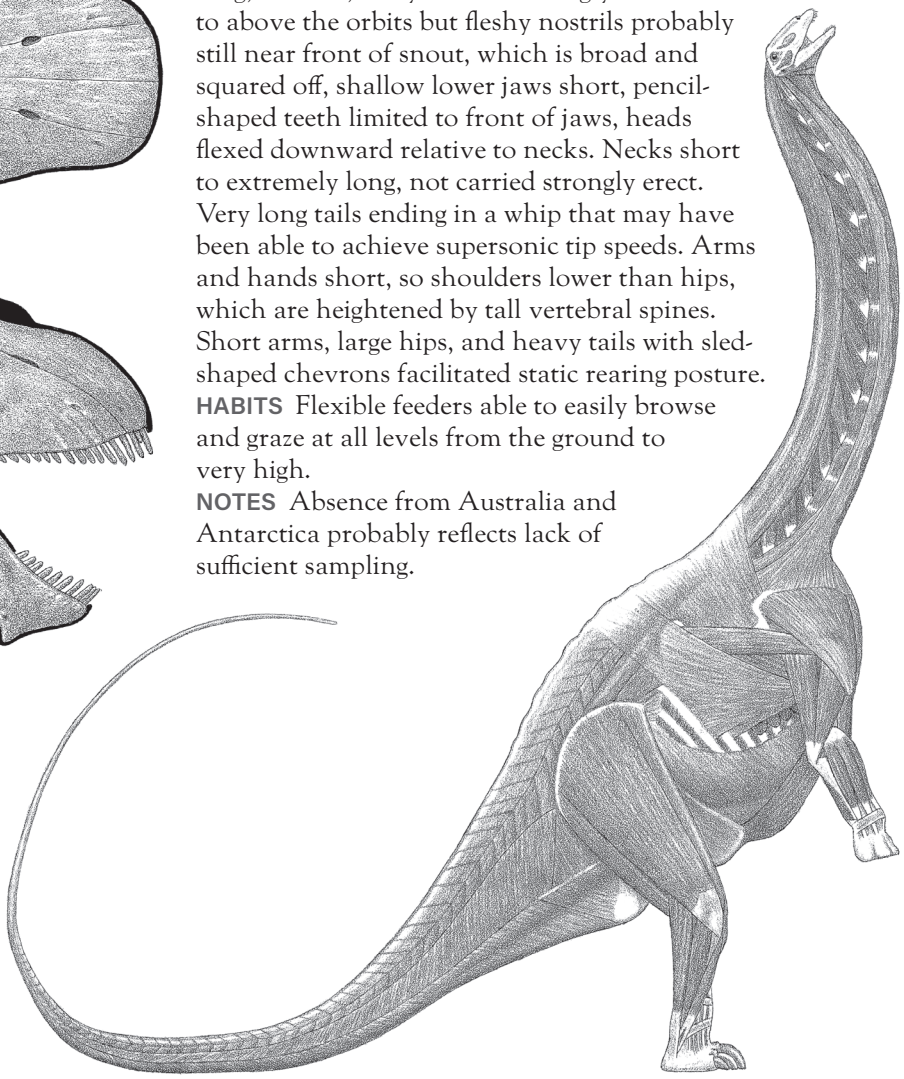
— DIPLODOCOIDS

SMALL (FOR SAUROPODS) TO GIGANTIC NEOSAUROPODS LIMITED TO THE EARLY JURASSIC TO THE EARLY LATE CRETACEOUS OF THE AMERICAS, EUROPE, AFRICA, ASIA.



Diplodocus shaded skull

ANATOMICAL CHARACTERISTICS Variable. Heads long, shallow, bony nostrils strongly retracted to above the orbits but fleshy nostrils probably still near front of snout, which is broad and squared off, shallow lower jaws short, pencil-shaped teeth limited to front of jaws, heads flexed downward relative to necks. Necks short to extremely long, not carried strongly erect. Very long tails ending in a whip that may have been able to achieve supersonic tip speeds. Arms and hands short, so shoulders lower than hips, which are heightened by tall vertebral spines. Short arms, large hips, and heavy tails with sled-shaped chevrons facilitated static rearing posture.
HABITS Flexible feeders able to easily browse and graze at all levels from the ground to very high.
NOTES Absence from Australia and Antarctica probably reflects lack of sufficient sampling.



Brontosaurus muscle study

REBBACHISAURIDS

SMALL AND MEDIUM-SIZED DIPLODOCOIDS LIMITED TO THE EARLY AND EARLY LATE CRETACEOUS OF SOUTH AMERICA AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Necks short by sauropod standards, neck ribs overlapping a little. Vertebral spines not forked. Upper scapula blades very broad.
NOTES The last radiation of diplodocids and nonmacronarian sauropods, fragmentary *Xenoposeidon proneneukos* from the Berriasian-Valanginian of England may be the earliest known example of this group. A fossil labeled *Maraapunisaurus* (was *Amphicoelias*) *fragillimus*—based on disintegrated colossal trunk vertebra up to 2.6 m (8.5 ft) tall from the Late Jurassic upper Morrison Formation—may be related to this group and suggests an animal of 80–120 tonnes.

Amazonsaurus maranhensis
— 12 m (40 ft) TL, 4.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Northern Brazil; Itapecuru.
NOTES The relationships of *Amazonsaurus* are uncertain.

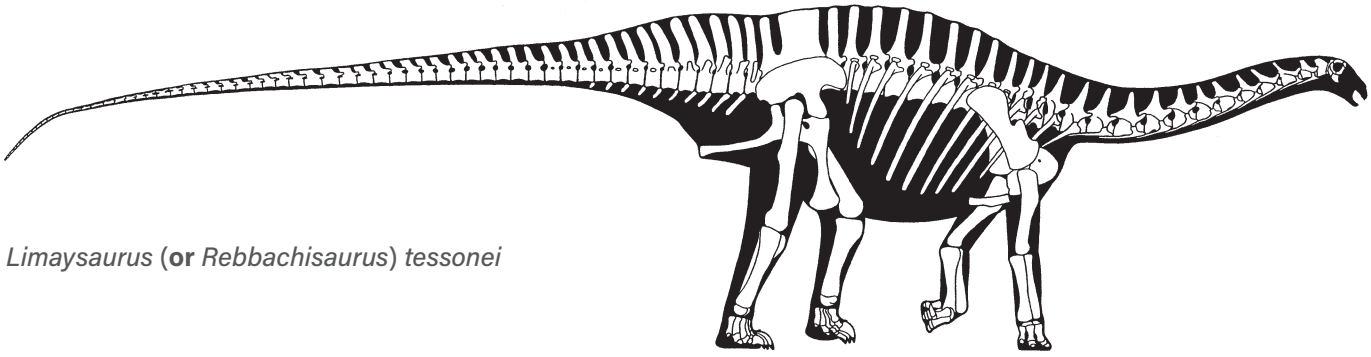
Zapalasaurus bonapartei
— 9 m (29 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Western Argentina; upper La Amarga.
HABITAT/S Well-watered coastal woodlands with short dry season.

Comahuesaurus windhauseni
— 12 m (40 ft) TL, 4.5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous; late Aptian and/or early Albian.
DISTRIBUTION AND FORMATION/S Western Argentina; Lohan Cura.
HABITAT/S Well-watered coastal woodlands with short dry season.

Rebbachisaurus (or *Rayosaurus*) *agrioensis*
— 10 m (33 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Western Argentina; Rayoso.
NOTES Whether *Rayosaurus*, *Rebbachisaurus*, and *Limaysaurus* are separate genera is uncertain.

Limaysaurus (or *Rebbachisaurus*) *tessonei*
— 15 m (50 ft) TL, 8 tonnes
FOSSIL REMAINS Minority of skull, majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck fairly deep. Tall vertebral spines over hips form a low sail. Chevrons may be absent from most of underside of tail.
AGE Early Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Rebbachisaurus garasbae
— 14 m (45 ft) TL, 7.4 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Hip sail tall.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Morocco; Tegana.



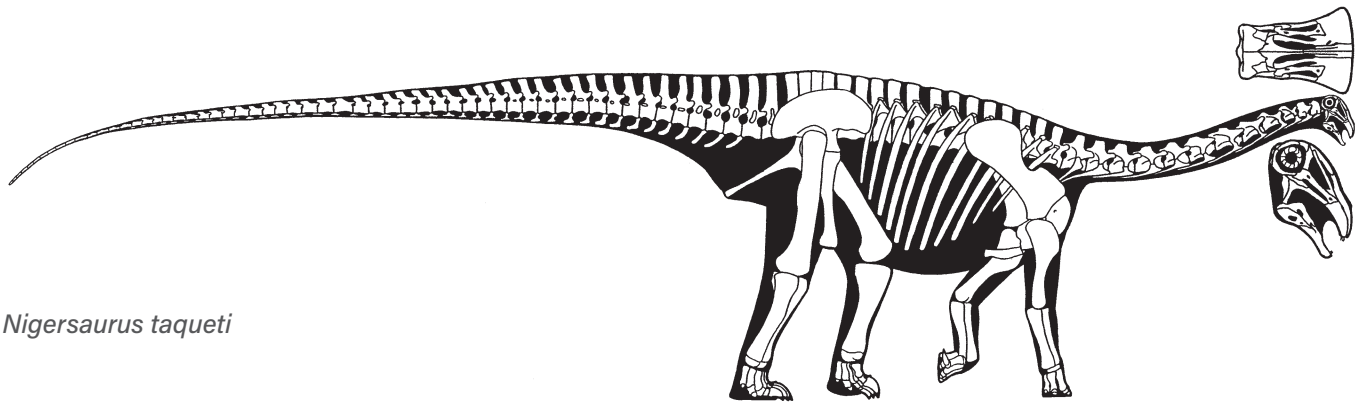
Limaysaurus (**or** *Rebbachisaurus*) *tessonei*

Cathartesaura anaerobica
— 12 m (40 ft) TL, 3 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Huincul.
HABITAT/S Well-watered woodlands with short dry season.
NOTES The last known diplodocid and nonmacronarian sauropod. This and *Rebbachisaurus* species may form subfamily Limaysaurinae.

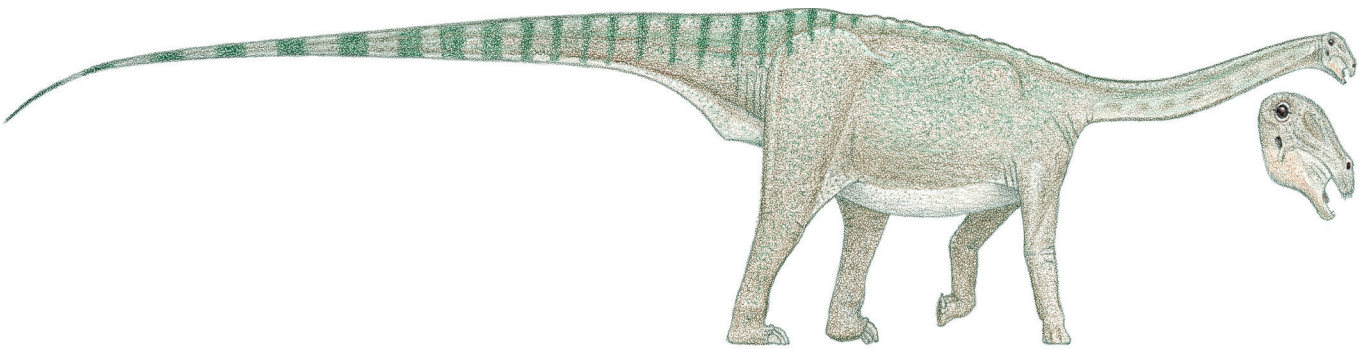
Demandasaurus darwini
— 9 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skull and skeletons, many isolated bones.
ANATOMICAL CHARACTERISTICS Neck short. Hip sail present.
AGE Early Cretaceous, late Barremian or early Aptian.
DISTRIBUTION AND FORMATION/S Spain; Castrillo de la Reina.
NOTES This, *Tataouinea*, and *Nigersaurus* may form subfamily Nigersaurinae.

Tataouinea hannibalis
— 14 m (45 ft) TL, 8 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Hip sail present.
AGE Early Cretaceous, early Albian.
DISTRIBUTION AND FORMATION/S Tunisia; Aïn el Guettar.
HABITAT/S Coastal.

Nigersaurus taqueti
— 9 m (30 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of skull, several partial skeletons, many isolated bones.
ANATOMICAL CHARACTERISTICS Head very lightly built, snout very broad and squared off, teeth limited to front rim of jaws, very numerous and rapidly replaced. Neck short, shallow. No hip sail.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Niger; upper Elrhaz.
HABITAT/S Coastal river delta.
HABITS Square muzzle at end of long neck was adaptation for mowing ground cover, also able to rear to high browse.
NOTES The most complex tooth battery among saurischians, mimics in some regards those of ornithischians except teeth were only for cropping plants. It is not known how many other rebbachisaurids shared these feeding adaptations. The other sauropod known to have a similarly broad and square beak is the titanosaur *Bonitasaura*.



Nigersaurus taqueti



— DICRAEOSAURIDS

SMALL (BY SAUROPOD STANDARDS) DIPLODOCOIDS LIMITED TO THE EARLY JURASSIC TO THE EARLY CRETACEOUS OF SOUTH AMERICA, AFRICA, AND ASIA.

ANATOMICAL CHARACTERISTICS Uniform. Necks short by sauropod standards, spines usually very tall, unable to elevate above shoulder level; ribs so short they do not overlap, increasing flexibility of neck. Tall vertebral spines over hips form a low sail. Most neck and trunk vertebral spines forked.
NOTES Absence from other continents may reflect lack of sufficient sampling.

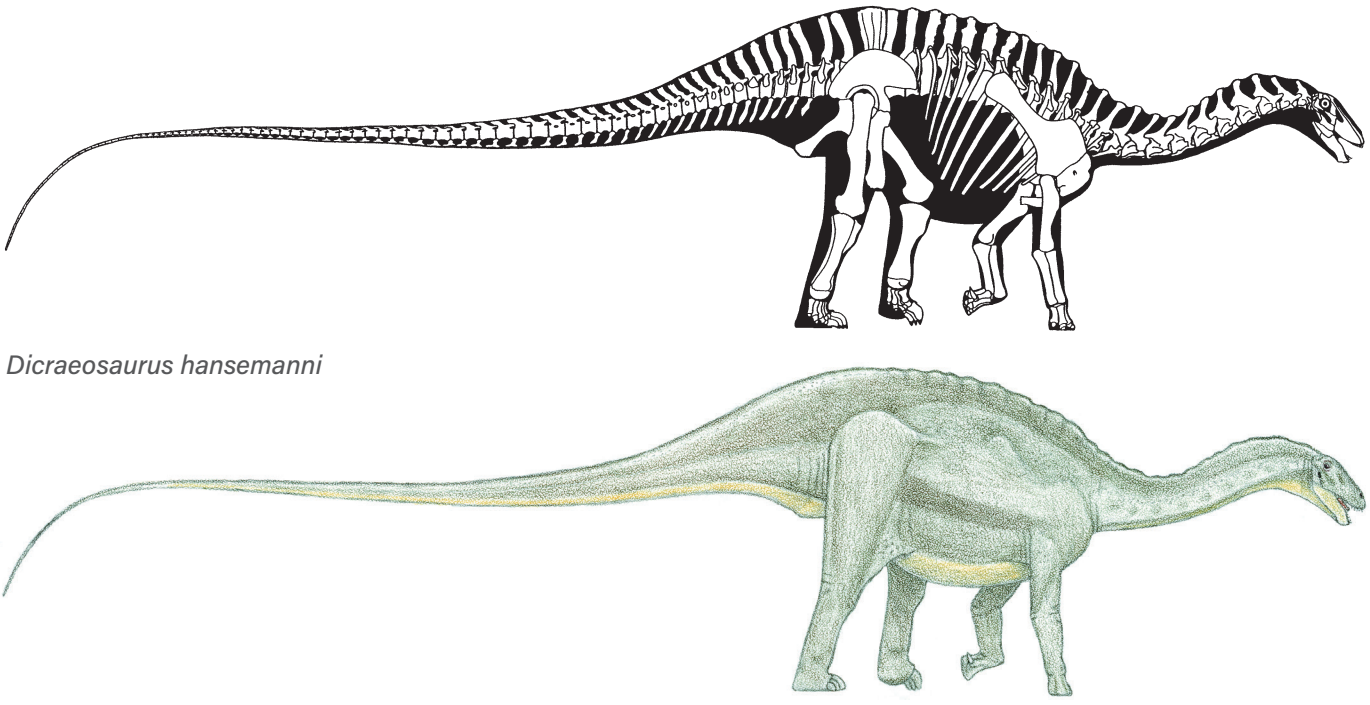
Lingwulong shenqi
— Adult size uncertain
FOSSIL REMAINS Minority of skull, partial skeleton, other partial remains.
ANATOMICAL CHARACTERISTICS Neck spines not tall.
AGE Early Jurassic, late Toarcian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yanan.

Suuwassea emilieae
— 15 m (50 ft) TL, 6 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Neck spines not tall.
AGE Late Jurassic, middle? Kimmeridgian.
DISTRIBUTION AND FORMATION/S Montana; probably middle Morrison.
HABITAT/S More coastal and wetter than rest of Morrison.
NOTES Relationships of this diplodocoid are uncertain.

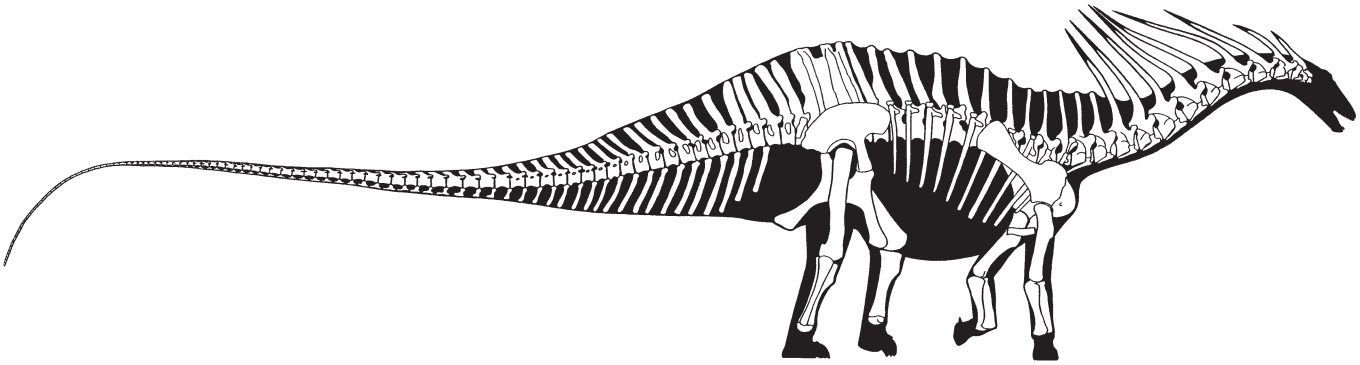
Brachytrachelopan mesai
— 10 m (35 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Neck short, spines not tall.
AGE Early Jurassic, middle Toarcian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Cañadón Asfalto.
NOTES The shortest-necked known sauropod.

Dicraeosaurus hansemanni
— 14 m (45 ft) TL, 5.5 tonnes
FOSSIL REMAINS Minority of skull, several skeletons from nearly complete to partial.
ANATOMICAL CHARACTERISTICS Lower jaw did not have contorted lower edge, as usually restored.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Tanzania; middle Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Remains from much earlier lower Tendaguru are not same taxon. May be an ancestor of *D. sattleri*.

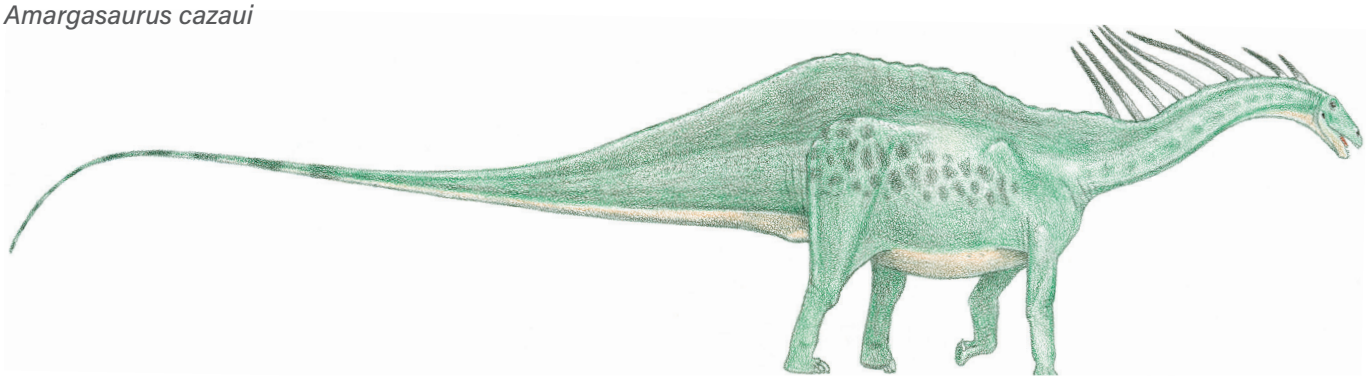
Dicraeosaurus? *sattleri*
— 15 m (50 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of skull, several partial skeletons.



Dicraeosaurus hansemanni



Amargasaurus cazaui



AGE Late Jurassic, late Kimmeridgian and/or early Tithonian.
DISTRIBUTION AND FORMATION/S Tanzania; upper Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES May not be the same genus as much earlier *D.hansemanni*.

Amargasaurus cazaui

— 13 m (43 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck vertebral spines elongated into very long spikes that may have been lengthened by horn sheaths. Hip sail tall.
AGE Late Early Cretaceous, early Barremian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower La Amarga.
HABITAT/S Well-watered coastal woodlands with short dry season.
HABITS Defense included arc of neck spines. Latter may have been used to generate clattering noise display.
NOTES *Amargatitanis macni* probably adult of this species. Has been suggested that the neck spikes supported sail fins, but this is not likely.

— DIPLODOCIDS

LARGE TO GIGANTIC DIPLODOCOIDS LIMITED TO THE MIDDLE JURASSIC TO EARLY CRETACEOUS OF NORTH AMERICA, EUROPE, AND AFRICA.

ANATOMICAL CHARACTERISTICS Variable. Necks long to extremely long, not able to elevate vertically, ribs so short they do not overlap, increasing flexibility of neck. Most neck and trunk vertebral spines forked. Tall vertebral spines over hips form a low sail. Tail whips very long.
NOTES If a diplodocid, fragmentary Argentinian *Leinkupal laticauda* extends group into early Early Cretaceous.

Amphicoelias altus

— 18 m (60 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Neck may not be elongated. Leg very slender by sauropod standards.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.

— DIPLODOCINES

LARGE TO GIGANTIC DIPLODOCIDS LIMITED TO THE MIDDLE AND LATE JURASSIC OF NORTH AMERICA, EUROPE, AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Lightly built. Necks very to extremely long, fairly slender. Tails very long. Femurs usually slender. Short vertical spikes appear to run atop vertebral series in at least some diplodocines.

Unnamed genus and species

— 22 m (71 ft) TL, 8.2 tonnes
FOSSIL REMAINS Virtually complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Femur robust.
AGE Late Jurassic, early late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lowermost Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Dyslocosaurus polyonychius

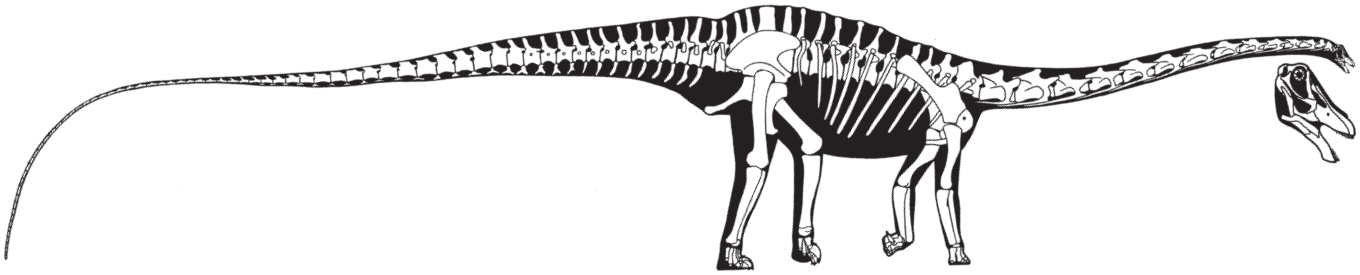
— 18 m (60 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Probably Late Jurassic.
DISTRIBUTION AND FORMATION/S Wyoming; probably Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Neither the formation this was found in nor its relationships are entirely certain.

Galeamopus (or *Diplodocus*) *hayi*

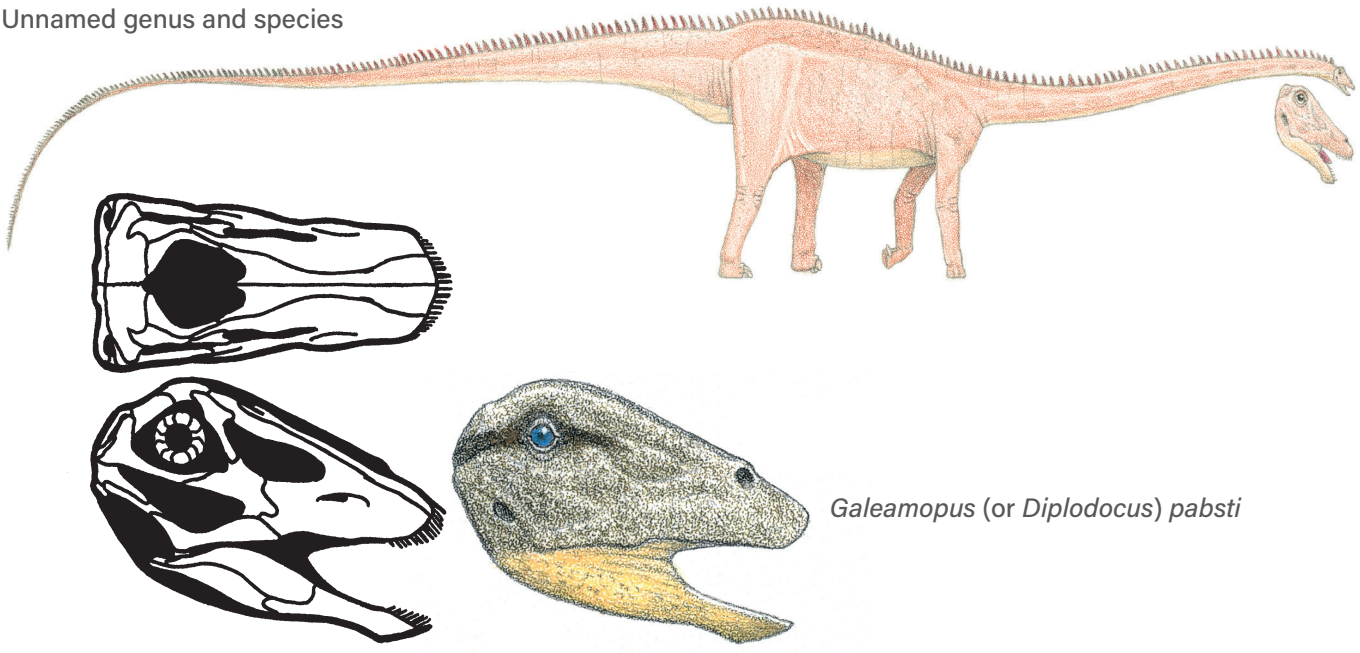
— Adult size uncertain
FOSSIL REMAINS Majority of an immature skeleton.
ANATOMICAL CHARACTERISTICS Neck very long. Tail extremely long.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES May be direct ancestor of G. *pabsti*.

Galeamopus (or *Diplodocus*) *pabsti*

— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton, partial skull.



Unnamed genus and species

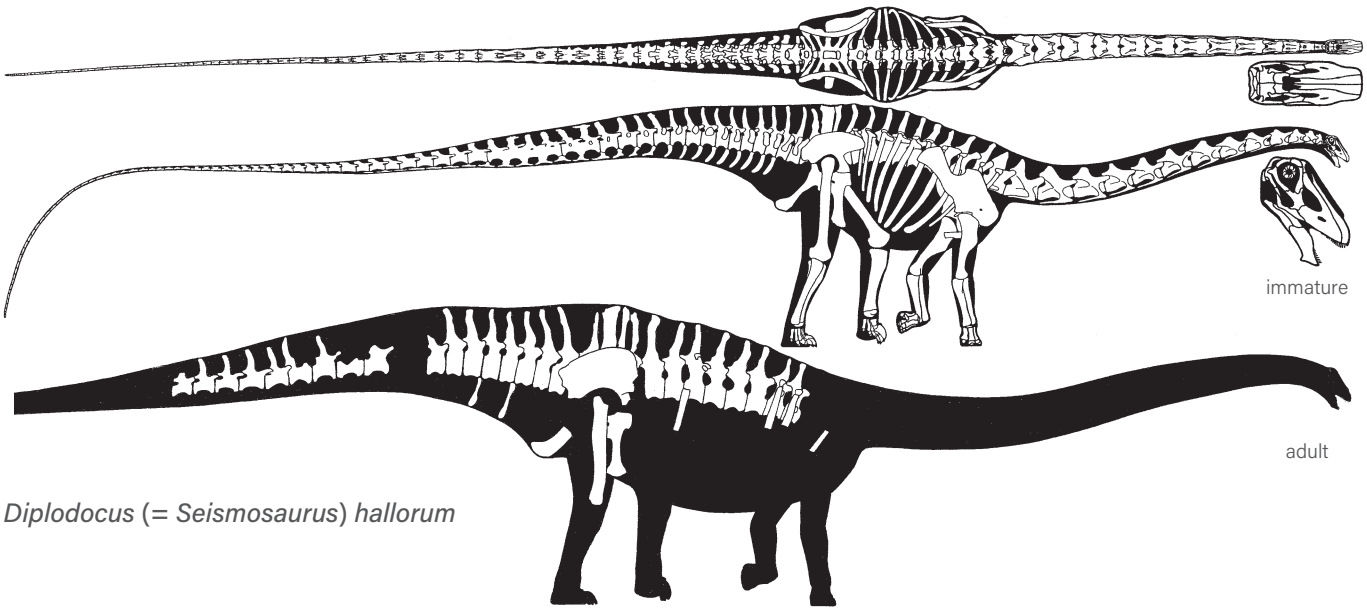


Galeamopus (or *Diplodocus*) *pabsti*

ANATOMICAL CHARACTERISTICS Neck very long.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming, Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Diplodocus (= *Seismosaurus*) *hallorum*

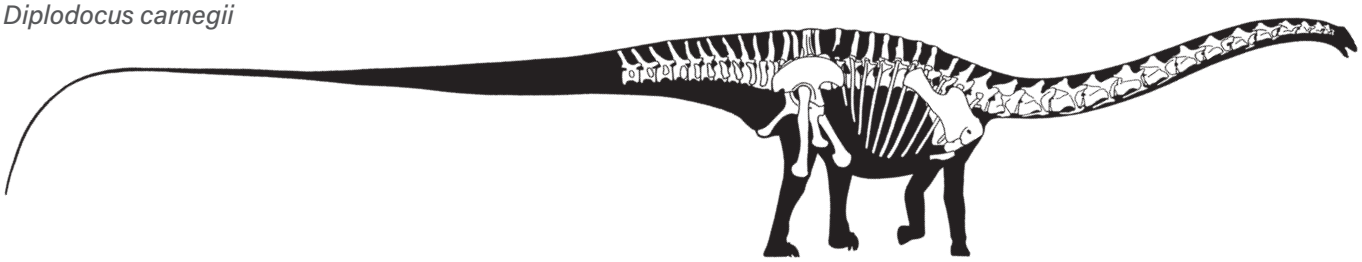
— 29 m (95 ft) TL, 23 tonnes
FOSSIL REMAINS Possible skull(s), fairly complete and partial skeletons.
ANATOMICAL CHARACTERISTICS Neck very long. Trunk compact. Tail extremely long. Femur slender until mature.
AGE Late Jurassic, early and/or early middle Kimmeridgian.



Diplodocus (= *Seismosaurus*) *hallorum*

Diplodocus and *Allosaurus*

Diplodocus carnegii



DISTRIBUTION AND FORMATION/S Colorado, Utah, New Mexico; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Many remains were placed in *D. longus*, but that is based on very fragmentary remains that may not be the same type as skeletons commonly placed in genus. The size of the largest "*Seismosaurus*" skeleton was greatly exaggerated. It is possible that the 22 m long, gracile-legged skeletons from the northern Morrison are a species distinct from the 29 m, apparently shorter-limbed *S. hallorum* from the southern Morrison.

Diplodocus carnegii

— 24 m (80 ft) TL, 12.5 tonnes
FOSSIL REMAINS Majority of several skeletons.
ANATOMICAL CHARACTERISTICS Neck very long. Trunk fairly long. Tail extremely long. Femur slender, at least at known sizes.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES It is possible this species grew as large as *D.hallorum*.

Tornieria (or *Barosaurus*) *africana*

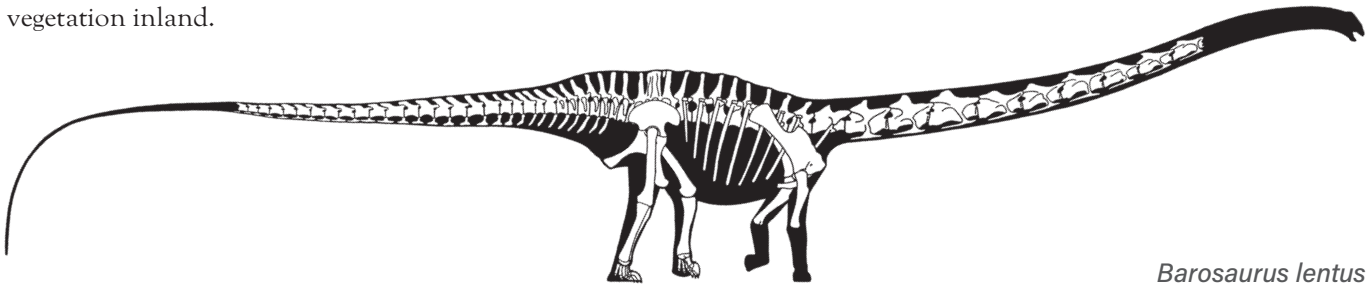
— 25 m (80 ft) TL, 10 tonnes
FOSSIL REMAINS Minority of skull and several skeletons.
ANATOMICAL CHARACTERISTICS Neck extremely long.
AGE Late Jurassic, late Kimmeridgian and/or early Tithonian.
DISTRIBUTION AND FORMATION/S Tanzania; upper Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Remains from much earlier middle Tendaguru are not same taxon.

Barosaurus lentus

— 27 m (88 ft) TL, 13.3 tonnes
FOSSIL REMAINS Possible partial skull, a few partial skeletons.
ANATOMICAL CHARACTERISTICS Neck extremely long. Tail moderately long.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S South Dakota, possibly Wyoming and Utah; middle Morrison.
HABITAT/S Northern near coastal portion of range, wetter than rest of Morrison.
HABITS High-level browser, although easily able to graze.
NOTES *Kaatedocus siberi* may belong to this taxon. Presence in more coastal portion of Morrison may be because of presence of taller trees. Partial remains suggest genus reached 30 tonnes.

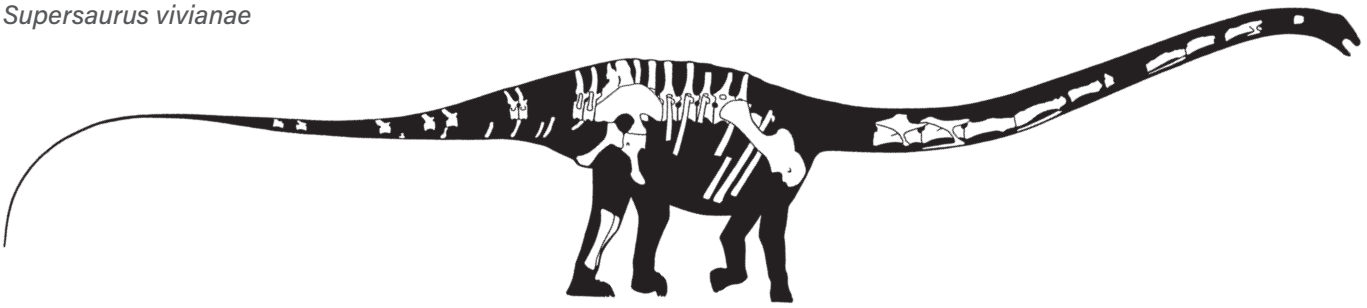
Supersaurus vivianae

— 38 m (125 ft) TL, 50 tonnes
FOSSIL REMAINS Minority of several skeletons.
ANATOMICAL CHARACTERISTICS More robustly built than other diplodocines. Neck very long.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Relationships to other diplodocids not entirely certain. Originally incorrectly thought to be the brachiosaur *Ultrasauros* (= *Ultrasaurus*). Estimates of greater bulk problematic.



Barosaurus lentus

Supersaurus vivianae



Supersaurus (= *Lourinhasaurus*) *alenquerensis*

— 18 m (60 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of several skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Portugal; Camadas de Alcobaça.
HABITAT/S Large, seasonally dry island with open woodlands.
NOTES May include *Dinheirosaurus lourinhanensis*.

— APATOSAURINES

GIGANTIC DIPLODOCIDS LIMITED TO THE LATE JURASSIC OF NORTH AMERICA.

ANATOMICAL CHARACTERISTICS Uniform. Skeletons massively constructed. Necks moderately long. Trunks very short. Tail whips very long. Pelves large to very large.
HABITS Flexible feeder from ground to highest levels. Built for pushing down trees. Powerful build indicates strong defense against predators.

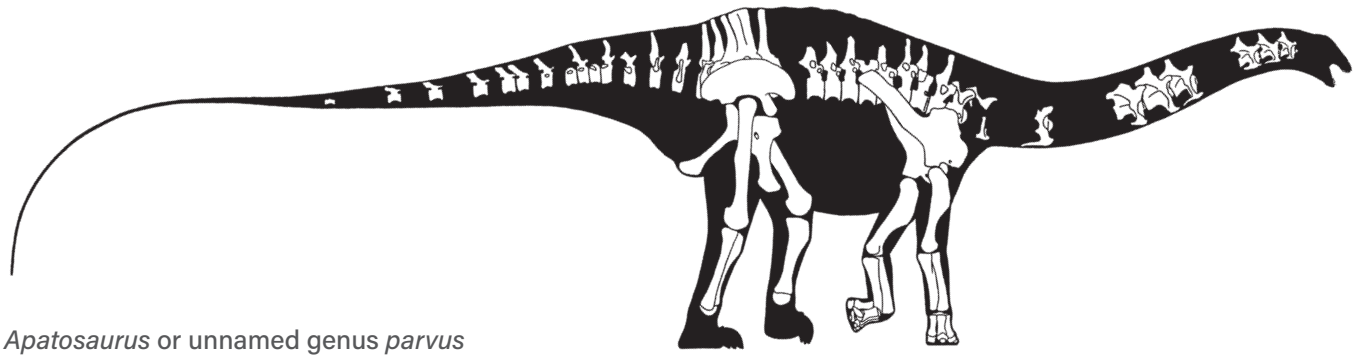
Unnamed genus and species

— 23 m (75 ft) TL, 13 tonnes
FOSSIL REMAINS Nearly complete skeleton.
ANATOMICAL CHARACTERISTICS Neck fairly long, not very broad. Hip sail not especially tall.
AGE Late Jurassic, early late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lowermost Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

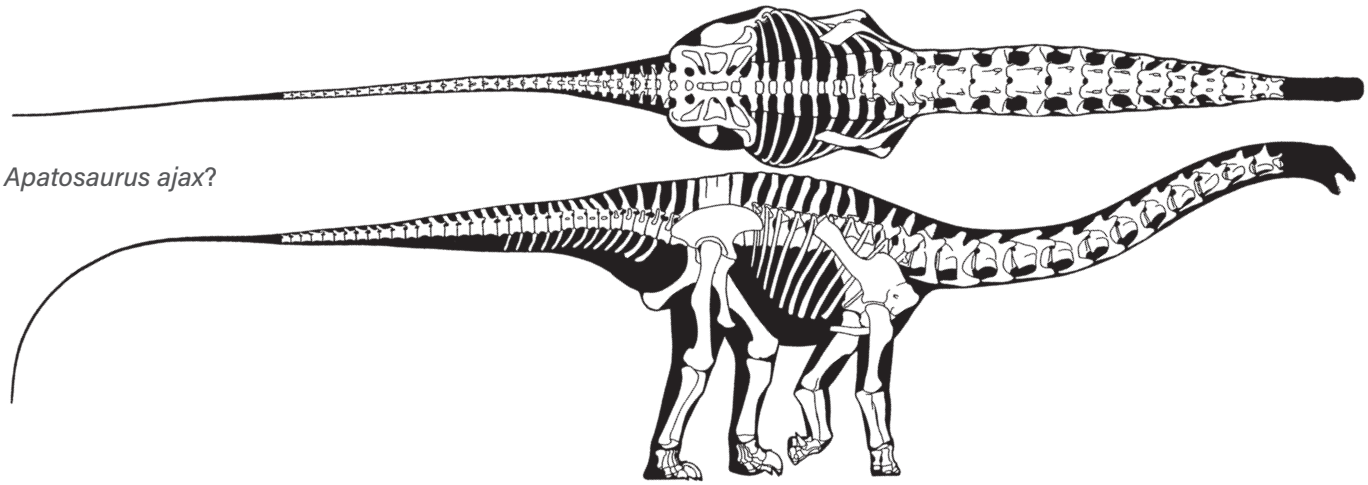
Apatosaurus or unnamed genus *parvus*

— 22 m (72 ft) TL, 15 tonnes
FOSSIL REMAINS Majority of skeletons, juvenile and adult.

Unnamed genus and species



Apatosaurus or unnamed genus *parvus*



Apatosaurus ajax?

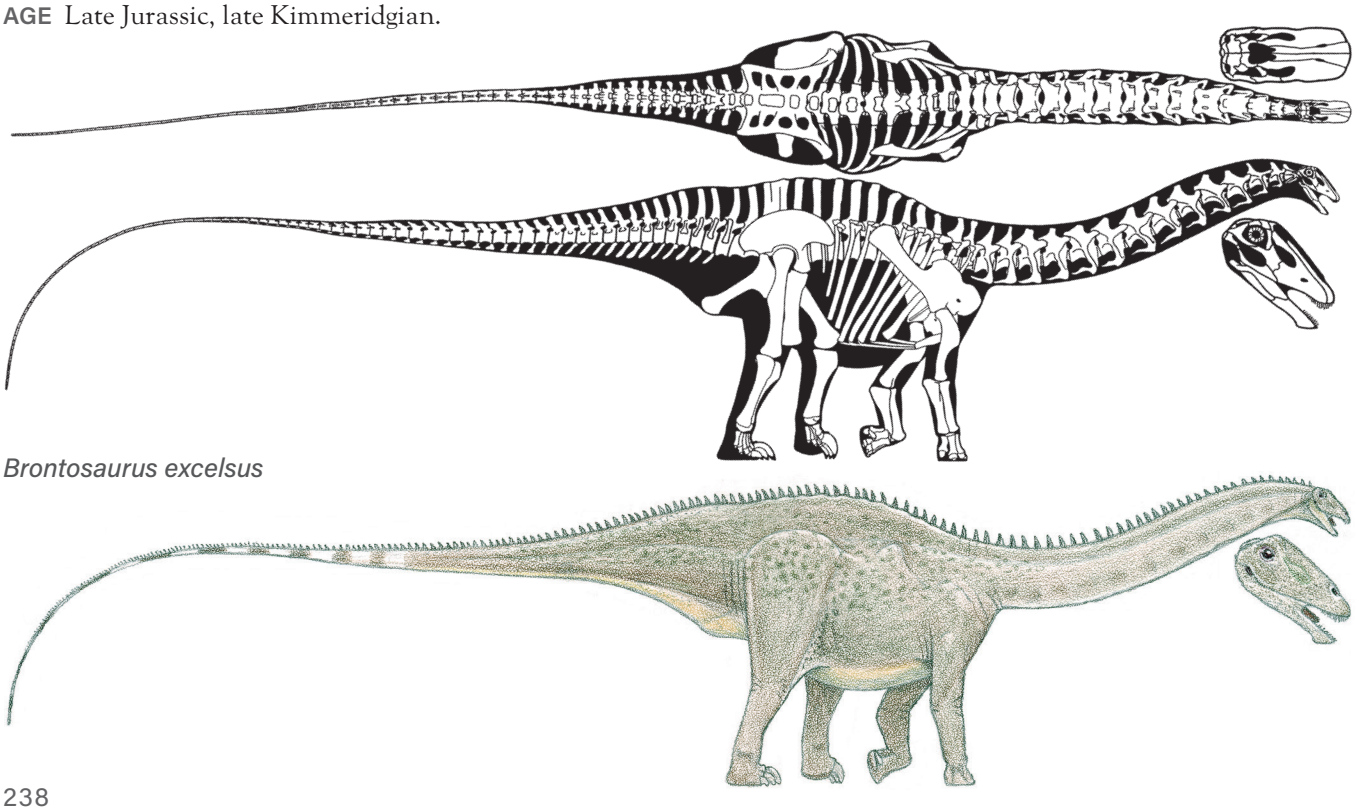
ANATOMICAL CHARACTERISTICS Neck moderately broad. Hip sail tall. Pelvis very large.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Not *Brontosaurus* because lacks its unusual downward and forward projections of cervical ribs, placement in later *Apatosaurus* problematic.

Apatosaurus ajax?

— 23 m (75 ft) TL, 22 tonnes
FOSSIL REMAINS Minority of skeleton, possibly nearly complete immature skeleton.
ANATOMICAL CHARACTERISTICS Neck apparently broad.
AGE Late Jurassic, late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado; upper and/or uppermost Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Broad neck best adapted for horizontal movements.
NOTES Validity of fragmentary original fossil problematic, as is placement of other fossils in this taxon.

Brontosaurus excelsus

— 23 m (75 ft) TL, 20 tonnes
FOSSIL REMAINS Possible nearly complete skull and a few skeletons, one almost complete.
ANATOMICAL CHARACTERISTICS Moderately broad neck very deep partly because of downward and forward projections of cervical ribs. Hip sail tall. Pelvis very large.
AGE Late Jurassic, middle Kimmeridgian.



Brontosaurus excelsus

DISTRIBUTION AND FORMATION/S Wyoming, Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Deep neck best adapted for vertical movements.
NOTES The classic sauropod. Very probably includes *B.louisae* because it shares with original fossil highly unusual downward cervical rib projections. Skull usually assigned to latter fossil may belong to a different apatosaurine. Largest land animal known from a nearly complete individual skeleton.

— MACRONARIANS

LARGE TO ENORMOUS NEOSAUROPODS OF THE MIDDLE JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Variable. Nostrils enlarged. Necks able to elevate subvertically. Hands elongated. Pubes broad.
NOTES Absence from Antarctica probably reflects lack of sufficient sampling.

— MACRONARIAN MISCELLANEA

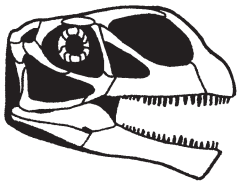
NOTES **The relationships of these macronarians are uncertain.**

Atlasaurus imelakei

— 15 m (50 ft) TL, 23 tonnes
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head broad and fairly shallow. Neck rather short. Tail not large. Arm and hand very long, and humerus almost as long as femur, so shoulder much higher than hips. Limbs long relative to size of body.
AGE Middle Jurassic, late Bathonian.
DISTRIBUTION AND FORMATION/S Morocco; Douar of Tazouda.
HABITAT/S Seasonally arid-wet coastline with tall trees limited to watercourses.
HABITS Medium- and high-level browser, not able to easily feed at ground level.
NOTES Its limbs proportionally longer than those of any other known sauropod, *Atlasaurus* emphasized leg over neck length to increase vertical reach to a greater extent than any other known member of the group. Has been placed in cetiosaurs, turiasaurs, and brachiosaurs.

Abrosaurus dongpoi

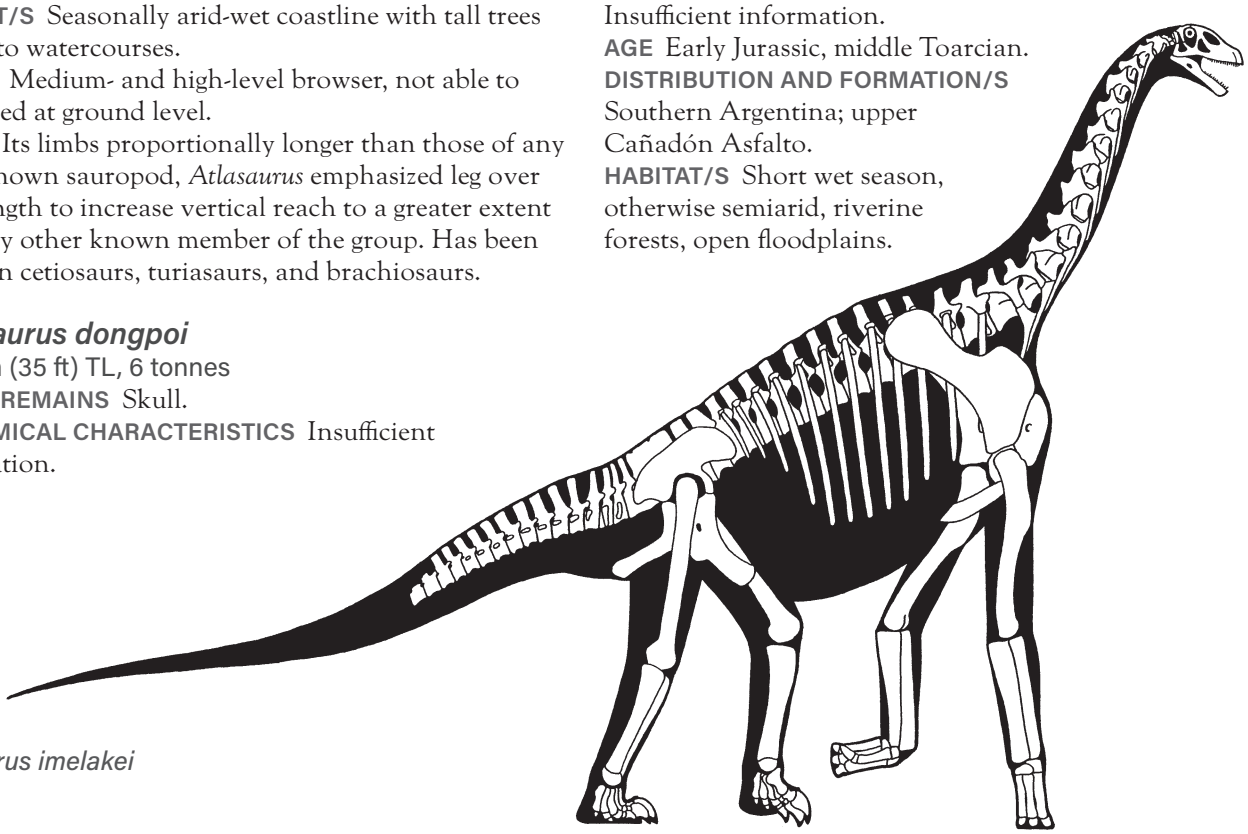
— 11 m (35 ft) TL, 6 tonnes
FOSSIL REMAINS Skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.



Abrosaurus dongpoi

Tehuelchesaurus benitezii

— 15 m (50 ft) TL, 18 tonnes
FOSSIL REMAINS Majority of skeleton, skin patches.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Jurassic, middle Toarcian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Cañadón Asfalto.
HABITAT/S Short wet season, otherwise semiarid, riverine forests, open floodplains.



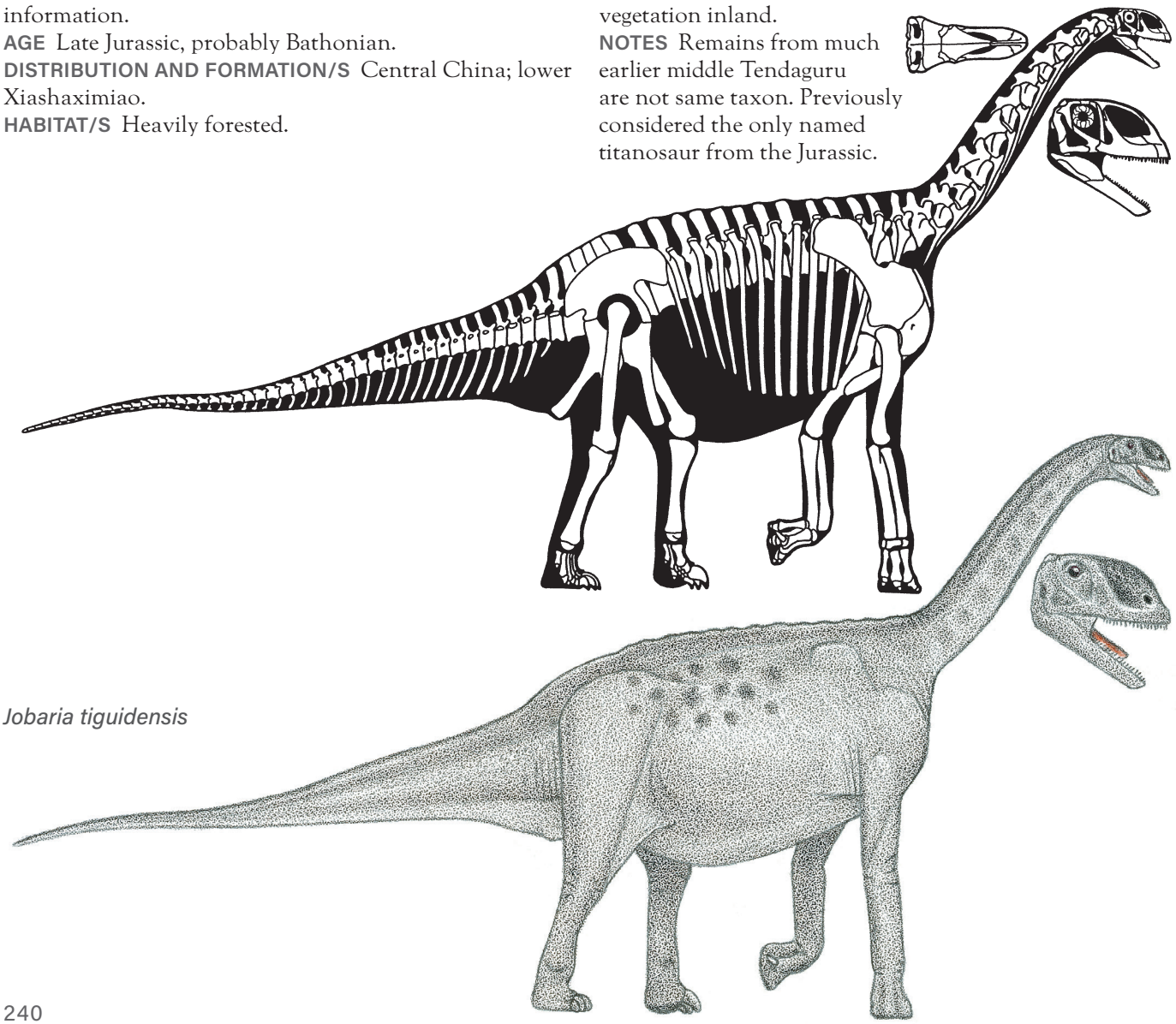
Atlasaurus imelakei

Jobaria tiguidensis
— 16 m (52 ft) TL, 18 tonnes
FOSSIL REMAINS Complete skull and several skeletons, nearly completely known.
ANATOMICAL CHARACTERISTICS Head not broad. Neck rather short. Tail moderately long. Arm and hand long, so shoulder higher than hip.
AGE Late Middle or early Late Jurassic.
DISTRIBUTION AND FORMATION/S Niger; Tiourarén.
HABITAT/S Well-watered woodlands.
HABITS Medium- and high-level browser, not able to feed easily at ground level.
NOTES Originally thought to be from the Early Cretaceous, the Tiourarén is from the later Jurassic. Relationships of *Jobaria* are uncertain, may not be a neosauropod.

Yuzhoulong qurenensis
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton, immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.

Bellusaurus sui
— Adult size uncertain
FOSSIL REMAINS Dozen and a half partial skeletons, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, middle Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; middle Shishugou.
NOTES May be a mamenchisaur.

Janenschia robusta
— 17 m (53 ft) TL, 20 tonnes
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Fingers and thumb claw present.
AGE Late Jurassic, late Kimmeridgian and/or early Tithonian.
DISTRIBUTION AND FORMATION/S Tanzania; upper Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Remains from much earlier middle Tendaguru are not same taxon. Previously considered the only named titanosaur from the Jurassic.

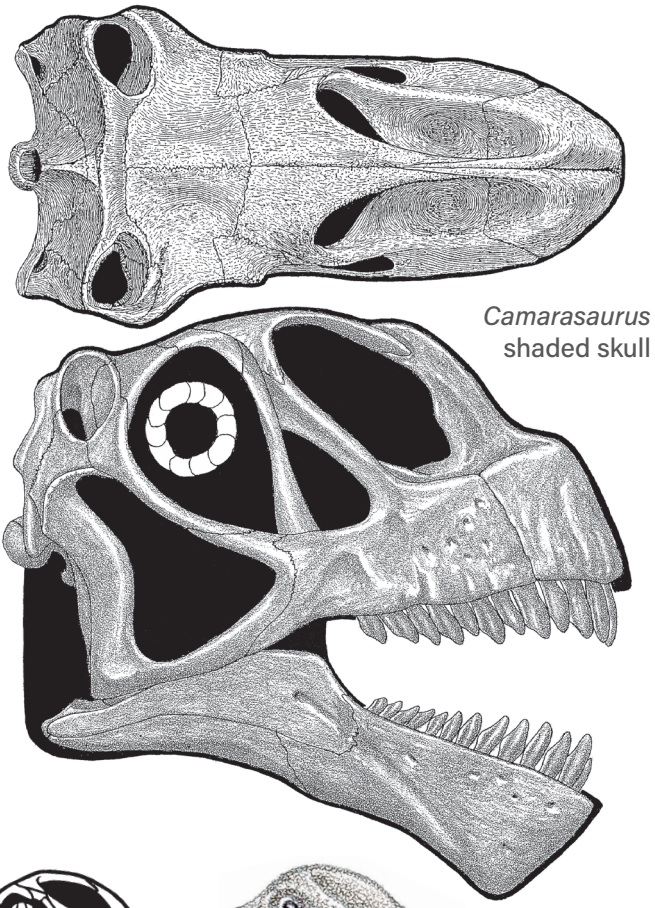


Jobaria tiguidensis

— CAMARASAURIDS

LARGE TO GIGANTIC MACRONARIAN SAUROPODS LIMITED TO THE LATE JURASSIC TO PERHAPS THE EARLY CRETACEOUS OF NORTH AMERICA AND EUROPE.

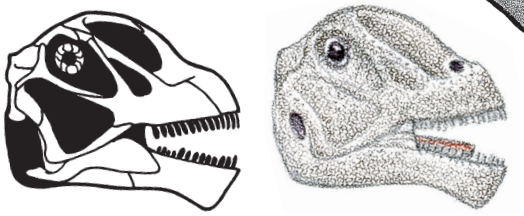
ANATOMICAL CHARACTERISTICS Uniform. Heads large for sauropods, deep, teeth fairly large. Necks rather short, shallow, broad. Most neck and trunk vertebral spines forked. Tails moderately long. Arms and hands long, so shoulders a little higher than hips. Front of pelves and belly ribs flare very strongly sideways so bellies are very broad and large. Retroverted pelves facilitated slow walking when rearing up by keeping hips and tails horizontal when bipedal.
HABITS Medium- and high-level browsers, unable to feed easily at ground level. Able to consume coarse vegetation.
NOTES Whether camarasaurs survived into the Early Cretaceous is uncertain.



Camarasaurus shaded skull

Camarasaurus grandis

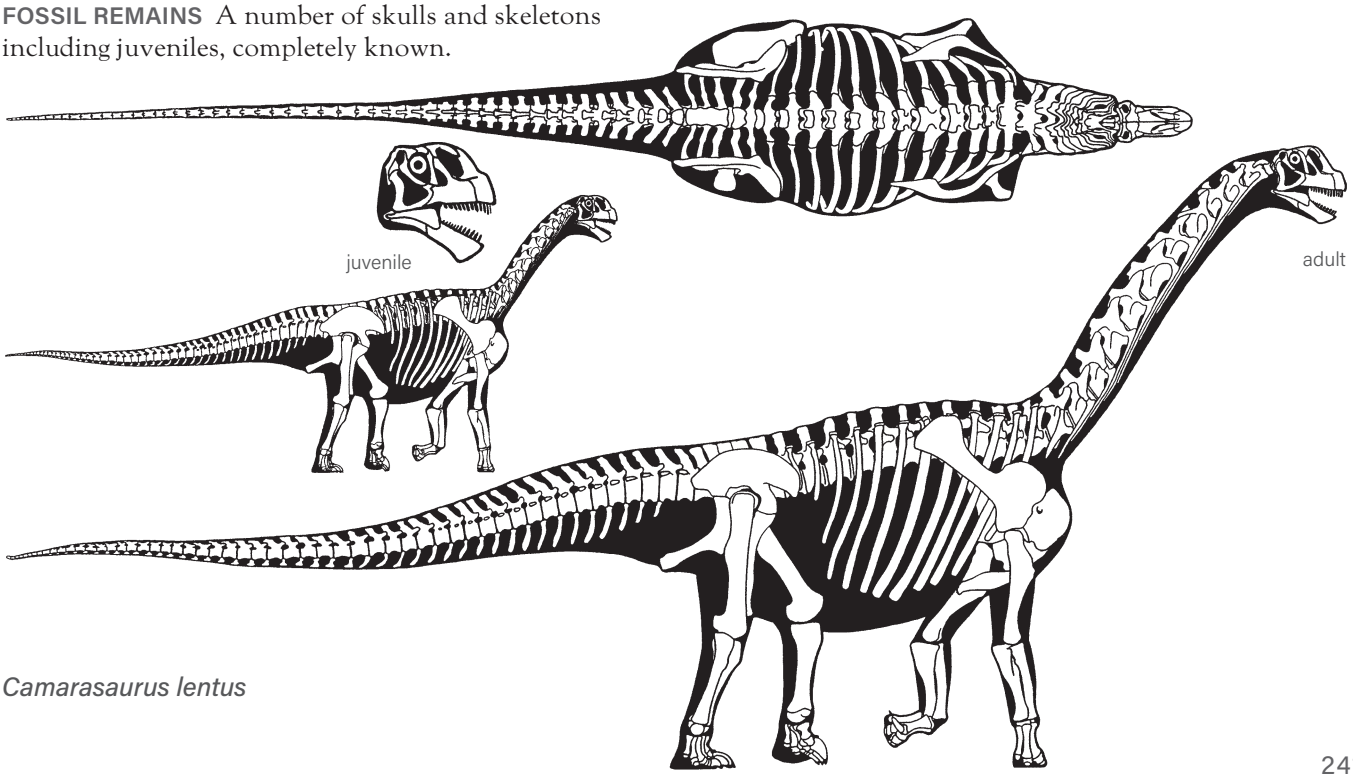
— 14 m (45 ft) TL, 13 tonnes
FOSSIL REMAINS A few skulls and majority of skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, early Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming, Colorado, Montana; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Apparently present earlier in the Middle Morrison than C. *lentus* and may be its direct ancestor.



Camarasaurus grandis

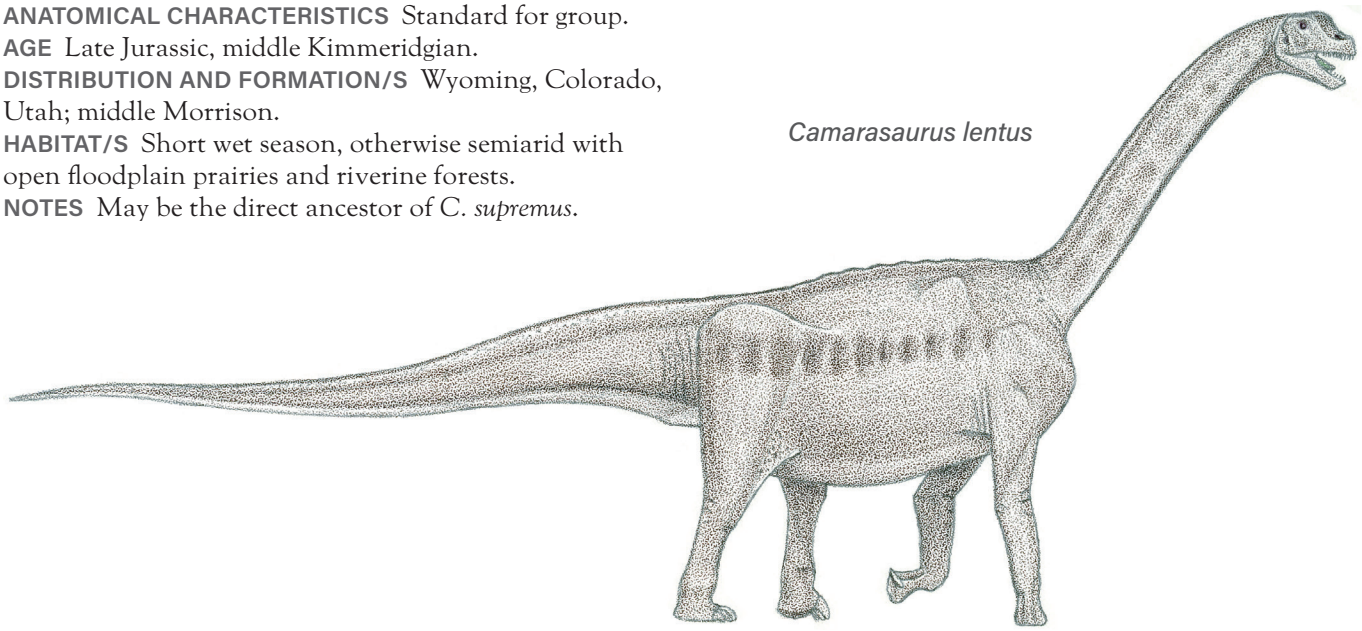
Camarasaurus lentus

— 15 m (50 ft) TL, 16 tonnes
FOSSIL REMAINS A number of skulls and skeletons including juveniles, completely known.



Camarasaurus lentus

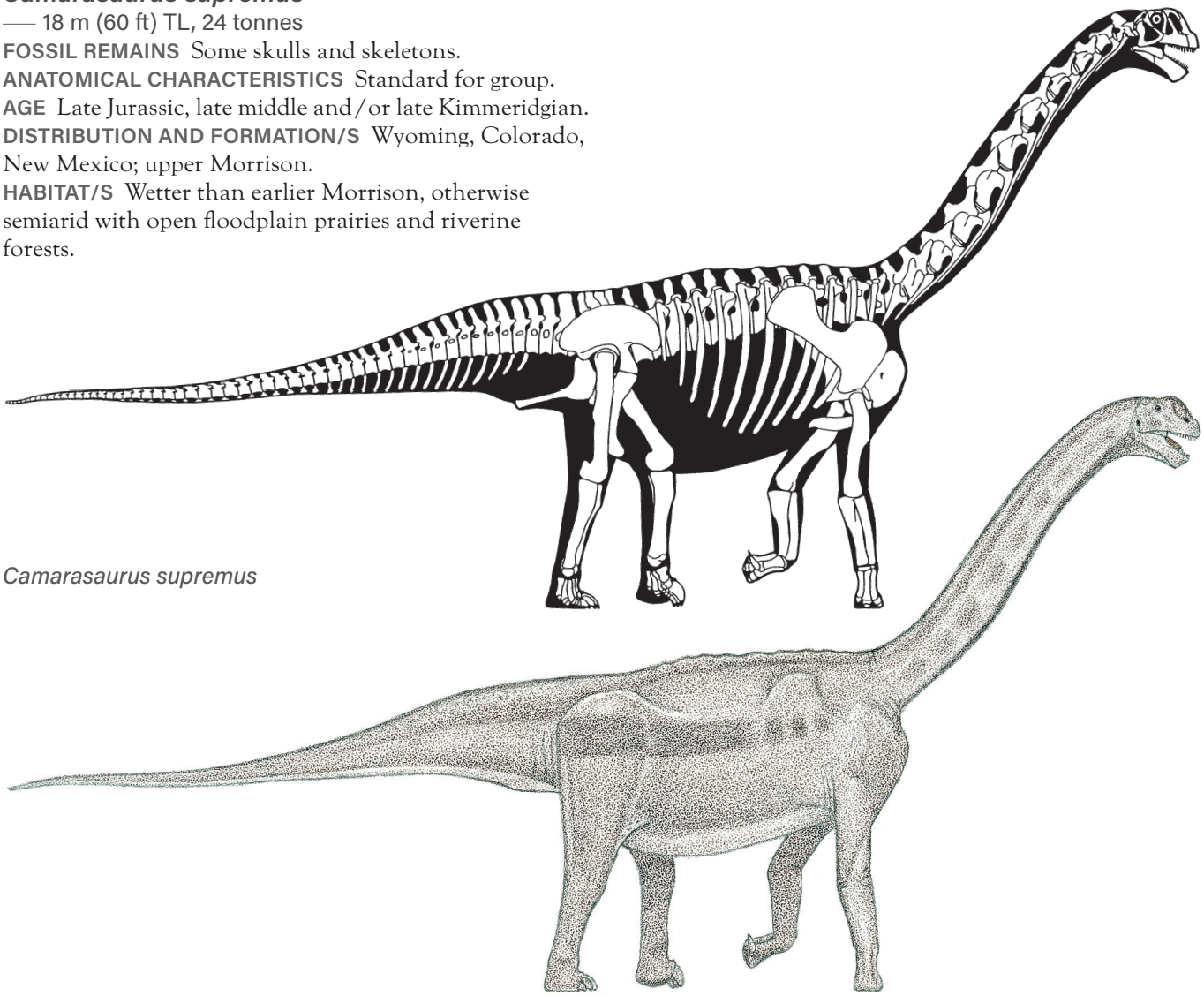
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming, Colorado, Utah; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES May be the direct ancestor of *C. supremus*.



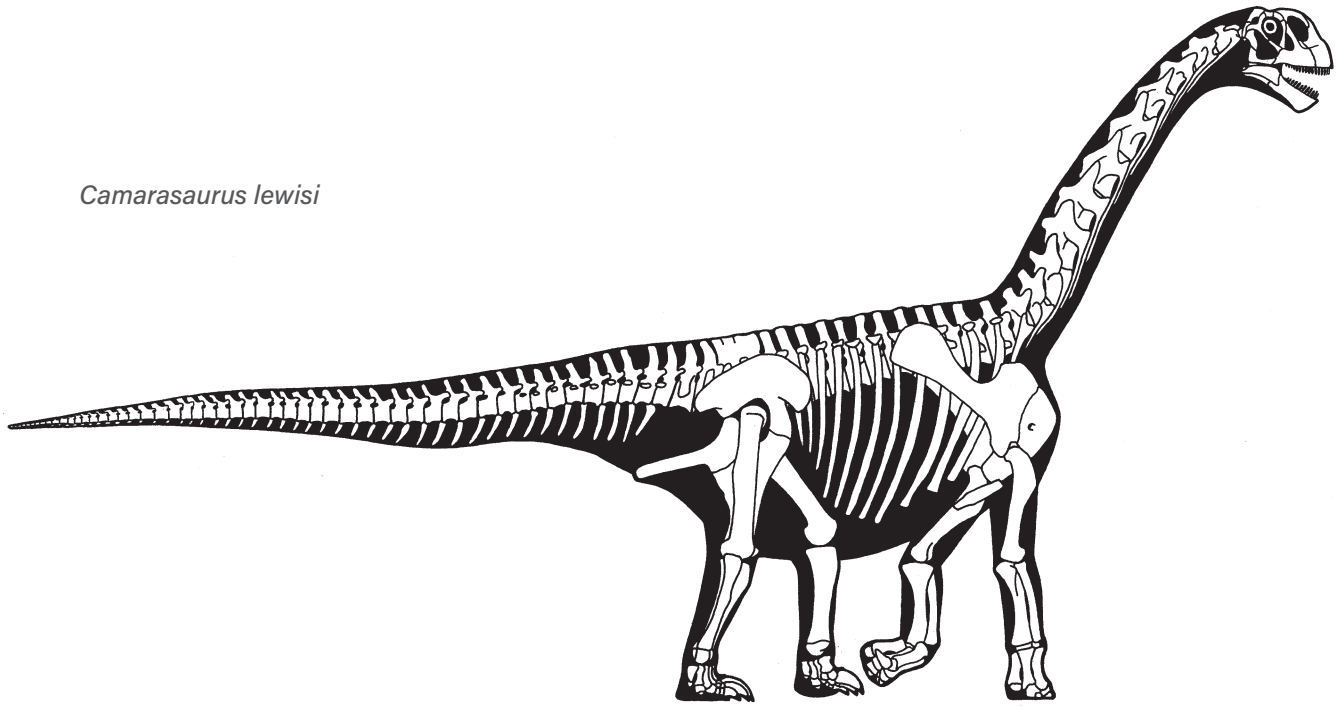
Camarasaurus lentus

Camarasaurus supremus

— 18 m (60 ft) TL, 24 tonnes
FOSSIL REMAINS Some skulls and skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming, Colorado, New Mexico; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.



Camarasaurus supremus



Camarasaurus lewisi

Camarasaurus (= *Cathetosaurus*) *lewisi*

— 13 m (43 ft) TL, 12 tonnes

FOSSIL REMAINS Majority of a skeleton, a complete skull and skeleton.

ANATOMICAL CHARACTERISTICS Modest sized. Head quite large, short, deep. Trunk short, belly deep. Pelvis deep, more strongly retroverted.

AGE Late Jurassic, early and/or early middle Kimmeridgian.

DISTRIBUTION AND FORMATION/S Colorado, Wyoming; middle Morrison.

HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

NOTES Head may have not been as relatively large in adults as in less mature examples. Best adapted among known sauropods for walking bipedally.

Aragosaurus ischiaticus

— 18 m (60 ft) TL, 25 tonnes

FOSSIL REMAINS Minority of skeleton.

ANATOMICAL CHARACTERISTICS Arm longer than that of *Camarasaurus*, so shoulder higher.

AGE Early Cretaceous, late Hauterivian and/or early Barremian.

DISTRIBUTION AND FORMATION/S Northern Spain; El Castellar.

HABITS High-level browser.

NOTES Relationships uncertain.

— TITANOSAURIFORMS

LARGE TO ENORMOUS MACRONARIAN SAUROPODS OF THE MIDDLE OR LATE JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Variable. Teeth elongated. Gauge of trackways broader than those of other sauropods. Front of pelves and belly ribs flare very strongly sideways, so bellies are very broad and large. Fingers further reduced or absent, thumb claws reduced or absent.

NOTES Absence from Antarctica probably reflects lack of sufficient sampling.

— TITANOSAURIFORM MISCELLANEA

NOTES The relationships of these titanosauriforms are uncertain.

AUSTRALODOCUS BOHETII

— 17 m (55 ft) TL, 4 tonnes

FOSSIL REMAINS Neck vertebrae.

ANATOMICAL CHARACTERISTICS Neck very long.

AGE Late Jurassic, late Kimmeridgian and/or early Tithonian.

DISTRIBUTION AND FORMATION/S Tanzania; upper Tendaguru.

HABITAT/S Coastal, seasonally dry with heavier vegetation inland.

NOTES Long considered a diplodocid.

Fusuisaurus zhaoi
— 22 m (70 ft) TL, 35 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Southern China; Napai.

Huanghetitan liujiaxiaensis
— 12 m (40 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Northern China; Haoling.

Dongbeititan dongi
— 15 m (59 ft) TL, 7 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Heavily constructed. Neck broad, moderately long.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Tastavinsaurus sanzi
— 16 m (50 ft) TL, 8 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Aptian.
DISTRIBUTION AND FORMATION/S Eastern Spain; Xert.

Fukuititan nipponensis
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Barremian.
DISTRIBUTION AND FORMATION/S Central Japan; Kitadani.

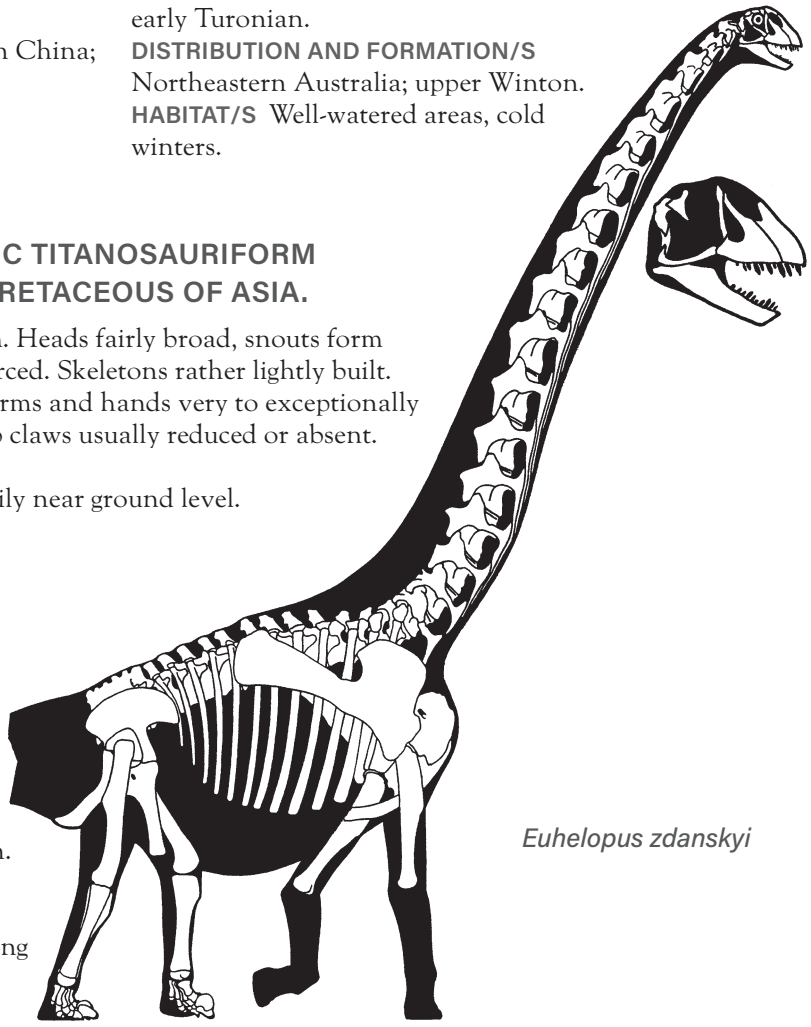
Wintonotitan wattsi
— 15 m (50 ft) TL, 10 tonnes
FOSSIL REMAINS Minority of two skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian and/or early Turonian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; upper Winton.
HABITAT/S Well-watered areas, cold winters.

— EUHELOPIDS

SMALL (FOR SAUROPODS) TO GIGANTIC TITANOSAURIFORM SAUROPODS OF THE EARLY OR LATE CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads fairly broad, snouts form a shelf below nostrils, which are very large and arced. Skeletons rather lightly built. Necks moderately to very long. Tails not large. Arms and hands very to exceptionally long, so shoulders much higher than hips, thumb claws usually reduced or absent. Pelves rather small, retroverted.
HABITS High-level browsers, not able to feed easily near ground level.
NOTES Contents of this family not certain.

Euhelopus zdanskyi
— 11 m (35 ft) TL, 3.8 tonnes
FOSSIL REMAINS Majority of skull and two skeletons.
ANATOMICAL CHARACTERISTICS Neck long. Vertebral spines near base of neck forked. Arm probably very long, so shoulder higher than hip.
AGE Early Cretaceous, Berriasian or Valanginian.
DISTRIBUTION AND FORMATION/S Eastern China; Mengyin.
NOTES Proportions of arm and leg uncertain. Long thought a Late Jurassic mamenchisaur relative, now often an Early Cretaceous titanosauriform.



Euhelopus zdanskyi

Erketu ellisoni
— 15 m (50 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck extremely long, with vertebrae more elongated than in any other sauropod.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Bayanshiree.
HABITS Probably a high browser.

Phuwiangosaurus sirindhornae
— 19 m (62 ft) TL, 17 tonnes
FOSSIL REMAINS Partial skeletons, juvenile and adult.
ANATOMICAL CHARACTERISTICS Neck moderately long, some vertebral spines forked.
AGE Early Cretaceous, Valanginian or Hauterivian.
DISTRIBUTION AND FORMATION/S Thailand; Sao Khua.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Tangvayosaurus hoffeti
— 19 m (62 ft) TL, 17 tonnes
FOSSIL REMAINS Two partial skeletons.
ANATOMICAL CHARACTERISTICS Skeleton robustly built.
AGE Early Cretaceous, late Aptian or Albian.
DISTRIBUTION AND FORMATION/S Laos; Grès Supérieurs.

Qiaowanlong kangxii
— 12 m (40 ft) TL, 6 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck long, vertebral spines forked.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.

Yunmenglong ruyangensis
— 20 m (65 ft) TL, 30 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck very long.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Eastern China; Haoling.

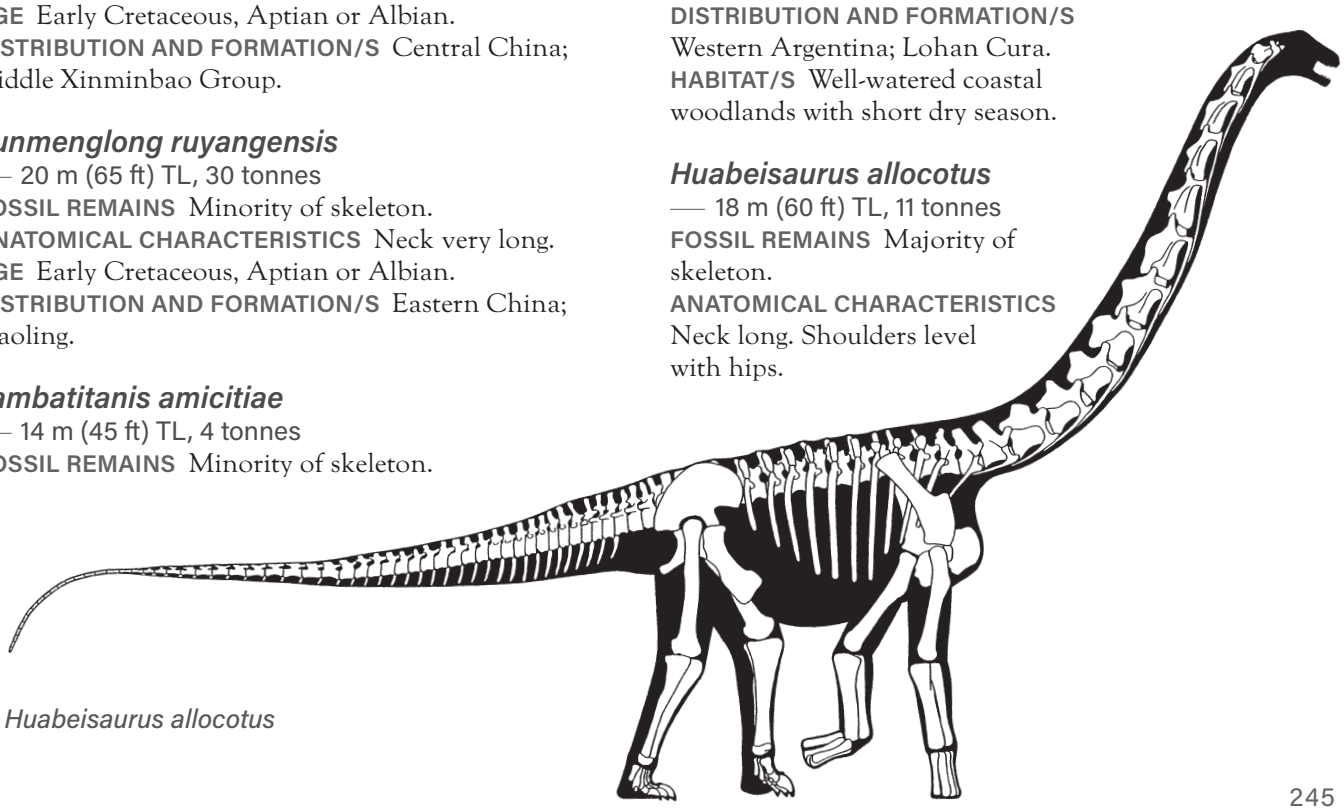
Tambatitanis amicitiae
— 14 m (45 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, probably early Albian.
DISTRIBUTION AND FORMATION/S Central Japan; lower Sasayama Group.

Daxiatitan binglingi
— Adult size not available
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Early Cretaceous.
DISTRIBUTION AND FORMATION/S Northern China; Hekou Group.

Jiangshanosaurus lixianensis
— 11 m (35 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Turonian or Coniacian.
DISTRIBUTION AND FORMATION/S Southeastern China; Jinhua.

Ligabuesaurus leanzai
— 18 m (60 ft) TL, 20 tonnes
FOSSIL REMAINS Minority of skull and two partial skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long. Spines of neck and trunk vertebrae very broad. Shoulder girdle appears to be relatively small, so shoulder may not have been high set despite long arm.
AGE Early Cretaceous, late Aptian or early Albian.
DISTRIBUTION AND FORMATION/S Western Argentina; Lohan Cura.
HABITAT/S Well-watered coastal woodlands with short dry season.

Huabeisaurus allocotus
— 18 m (60 ft) TL, 11 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck long. Shoulders level with hips.



Huabeisaurus allocotus

AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Northern China; upper Huiquanpu.
NOTES Relationships uncertain; if a euhelopid, indicates presence of group in Late Cretaceous.

Ruyangosaurus giganteus

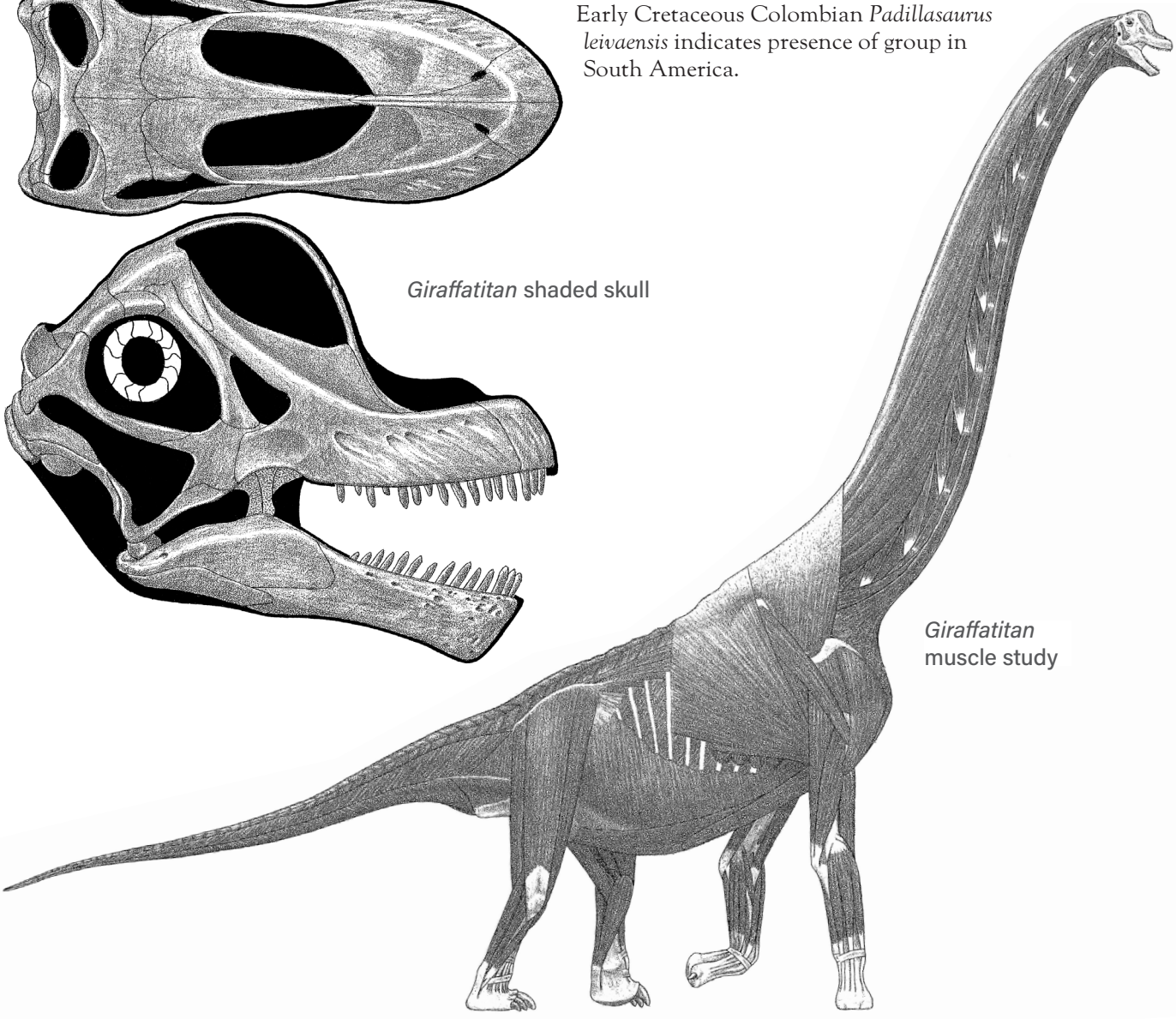
— 25 (80 ft) TL, 35 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Eastern China; Haoling.
NOTES Relationships uncertain.

— BRACHIOSAURIDS

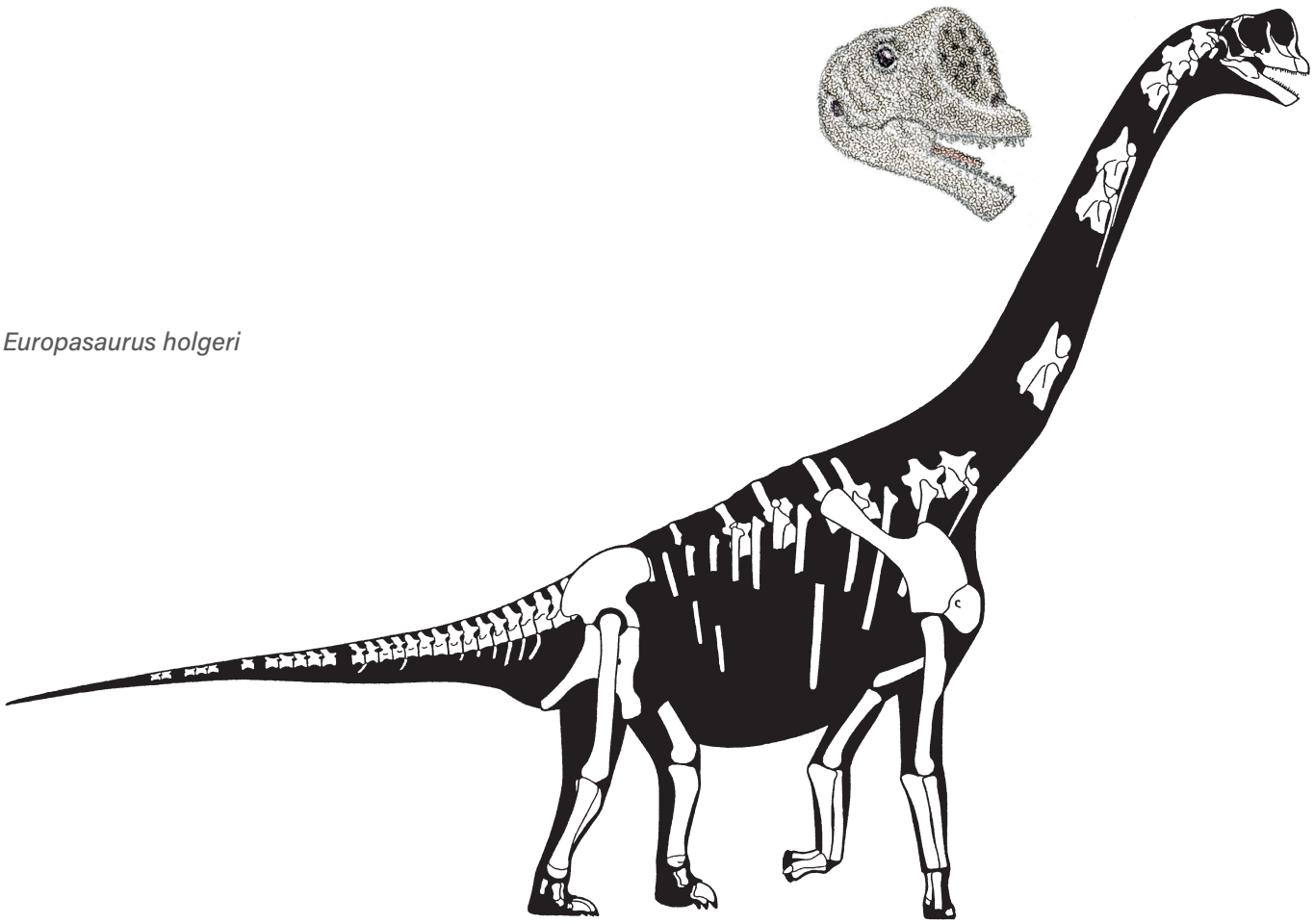
SMALL (FOR SAUROPODS) TO ENORMOUS TITANOSAURIFORM SAUROPODS LIMITED TO THE LATE JURASSIC AND EARLY CRETACEOUS OF THE AMERICAS, EUROPE, AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads fairly broad, snouts form shelf below nostrils, which are very large and arced. Skeletons rather lightly built. Necks moderately to very long. Tails not large. Arms and hands very to exceptionally long, so shoulders much higher than hips. Thumb claws reduced or absent. Pelves rather small, retroverted.
HABITS High-level browsers, not able to feed easily near ground level. Reared up less often than other sauropods. Fragmentary Early Cretaceous Colombian *Padillasaurus leivaensis* indicates presence of group in South America.

Giraffatitan shaded skull



Giraffatitan muscle study



Europasaurus holgeri

Vouivria damparisensis

— 15 m (50 ft) TL, 10 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late middle and/or early late Oxfordian.
DISTRIBUTION AND FORMATION/S Eastern France; Calcaires de Clerval.

Europasaurus holgeri

— 5.7 m (19 ft) TL, 830 kg (1,800 lb)
FOSSIL REMAINS Majority of skull and a number of skeletons.
ANATOMICAL CHARACTERISTICS Snout shelf short. Neck moderately long. Thumb claw small.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Northern Germany; Mittlere Kimmeridge-Stufe.
HABITS Small size limited browsing height.
NOTES Found as drift in nearshore marine sediments set amid islands, small size is probably dwarfism forced by limited food resources. May not be a brachiosaurid.

Brachiosaurus altithorax

— 22 m (72 ft) TL, 38 tonnes
FOSSIL REMAINS Minority of skeleton, possible partial skull, other bones.
ANATOMICAL CHARACTERISTICS Tail short for sauropods. Arm and hand exceptionally long, and humerus longer than femur, so shoulder very high.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Probably includes *Dystylosaurus edwini*. Some Morrison brachiosaur remains are more similar to *Giraffatitan*.

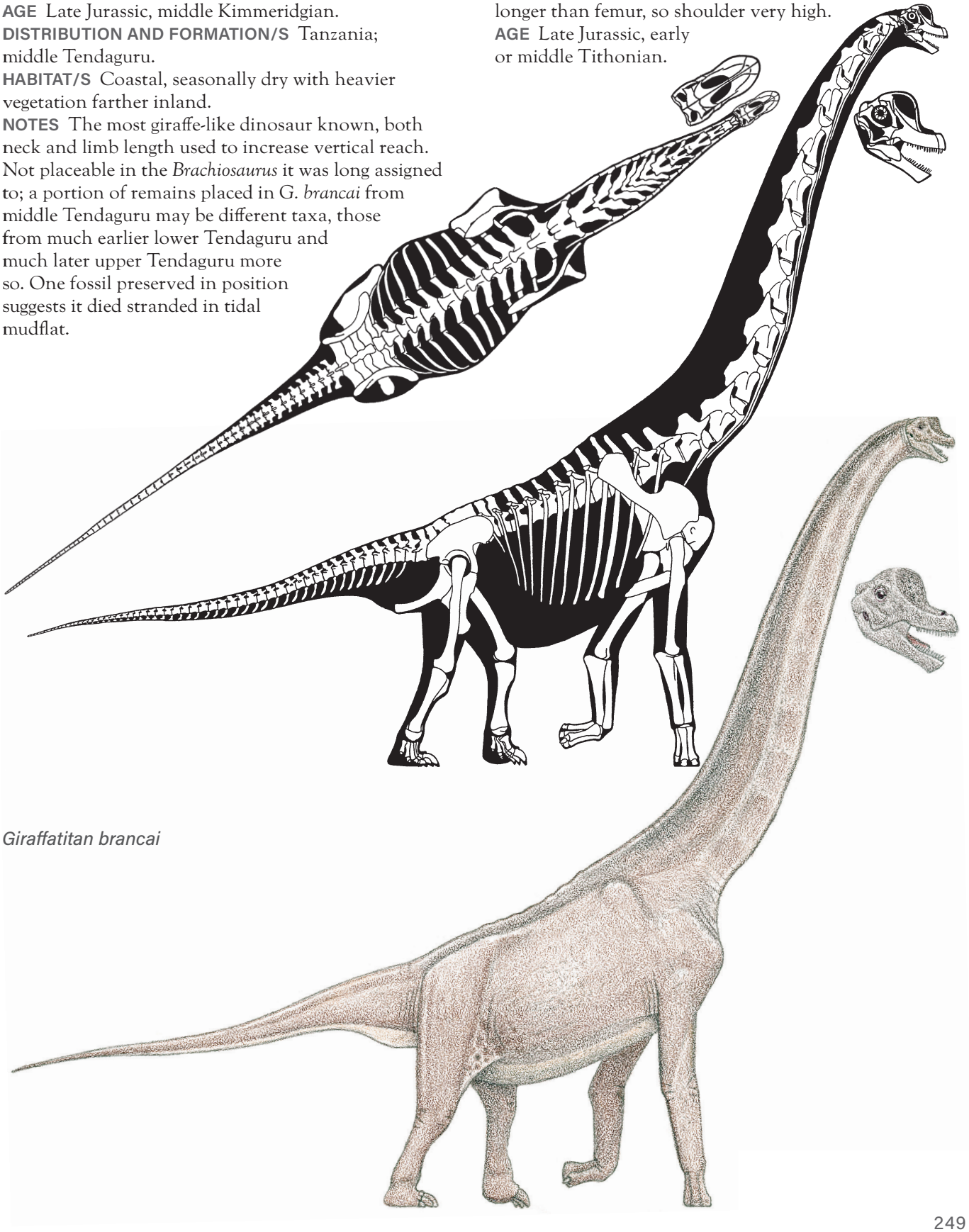
Giraffatitan brancai

— 25 m (80 ft) TL, 45 tonnes
FOSSIL REMAINS At least one partial skull and skeleton, possibly other skulls and skeletons.
ANATOMICAL CHARACTERISTICS Snout shelf long, head a little hourglass shaped in top view. Neck very long. Tall withers at shoulder anchored unusually deep neck ligaments and tendons. Back trunk vertebrae

Brachiosaurus

relatively small. Tail short for sauropods. Arm and hand exceptionally long, and humerus longer than femur, so shoulder very high, limb long relative to body. Thumb claw small.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Tanzania; middle Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation farther inland.
NOTES The most giraffe-like dinosaur known, both neck and limb length used to increase vertical reach. Not placeable in the *Brachiosaurus* it was long assigned to; a portion of remains placed in *G. brancai* from middle Tendaguru may be different taxa, those from much earlier lower Tendaguru and much later upper Tendaguru more so. One fossil preserved in position suggests it died stranded in tidal mudflat.

Lusotitan atalaiensis
— 21 m (70 ft) TL, 25 tonnes
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Humerus longer than femur, so shoulder very high.
AGE Late Jurassic, early or middle Tithonian.



Giraffatitan brancai

DISTRIBUTION AND FORMATION/S Portugal; middle Lourinhã.
HABITAT/S Large, seasonally dry island with open woodlands.
NOTES Relationships of *Lusotitan* uncertain. The presence of this and other gigantic sauropods on a Portuguese island shows that dwarfism was not occurring, perhaps because of intermittent immigration from nearby continents.

Galvesaurus herreroi
— Adult size uncertain
FOSSIL REMAINS Minority of several skeletons.
ANATOMICAL CHARACTERISTICS Neck long.
AGE Late Jurassic, late Kimmeridgian and/or early Tithonian.
DISTRIBUTION AND FORMATION/S Eastern Spain; lower Villar del Arzobispo.
NOTES Subadult remains indicate a very large sauropod.

Cedarosaurus weiskopfae
— 15 m (50 ft) TL, 10 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Neck length uncertain.
AGE Early Cretaceous, upper Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

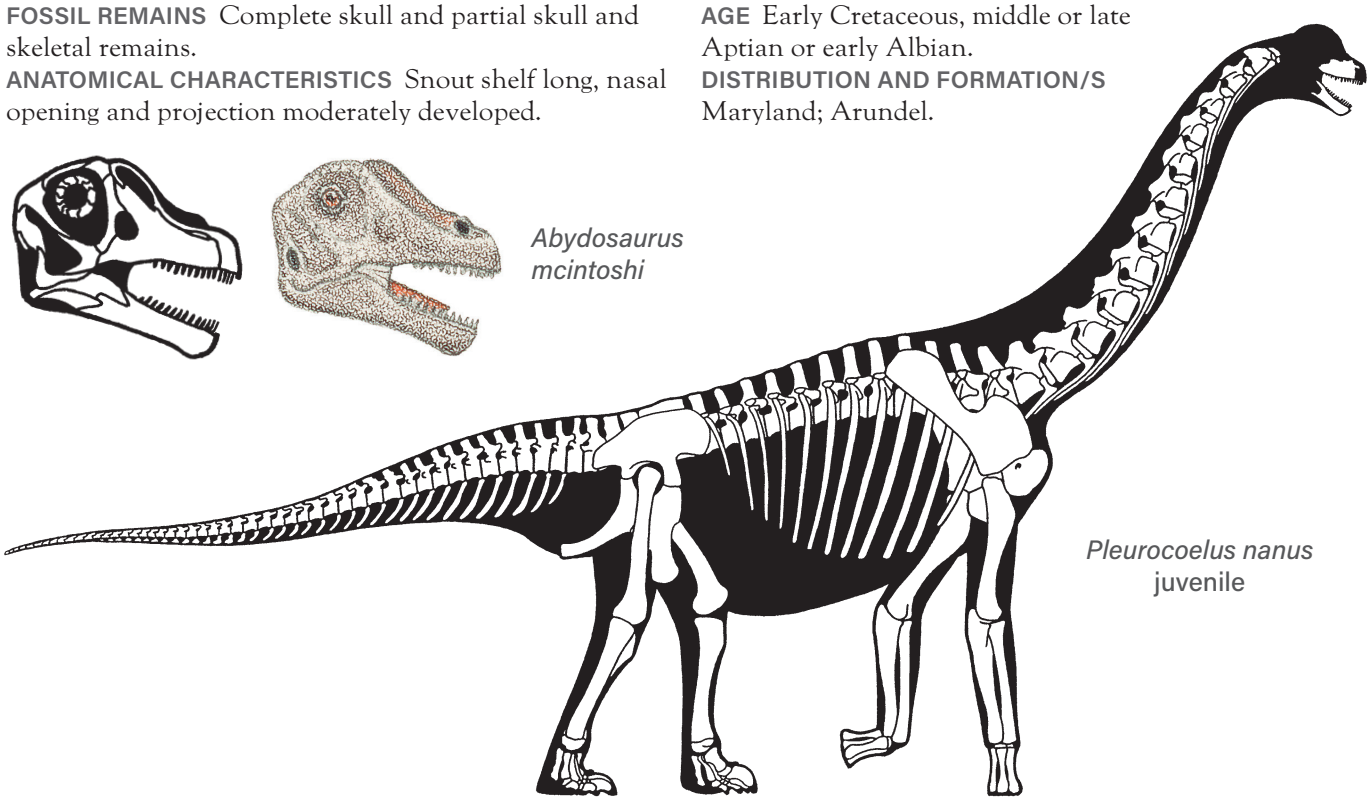
Abydosaurus mcintoshi
— Adult size uncertain
FOSSIL REMAINS Complete skull and partial skull and skeletal remains.
ANATOMICAL CHARACTERISTICS Snout shelf long, nasal opening and projection moderately developed.
AGE Early Cretaceous, upper Albian.
DISTRIBUTION AND FORMATION/S Utah; middle Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Sonorasaurus thompsoni
— 15 m (50 ft) TL, 10 tonnes
FOSSIL REMAINS Small minority of skeleton(s).
ANATOMICAL CHARACTERISTICS Toe claws reduced.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Arizona; middle Turney Ranch.

Venenosaurus dicrocei
— 12 m (40 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Utah; middle Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Pleurocoelus nanus
— Adult size uncertain
FOSSIL REMAINS Minority of a few juvenile skulls and skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long in juveniles.
AGE Early Cretaceous, middle or late Aptian or early Albian.
DISTRIBUTION AND FORMATION/S Maryland; Arundel.

Abydosaurus mcintoshi



Pleurocoelus nanus juvenile

NOTES Originally *Astrodon johnstoni* based on inadequate remains.

Sauroposeidon proteles
— 27 m (90 ft) TL, 45 tonnes
FOSSIL REMAINS Several partial skeletons.
ANATOMICAL CHARACTERISTICS Neck very long.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Texas, Oklahoma; Antlers, Paluxy, Glen Rose.
HABITAT/S Floodplain with coastal swamps and marshes.
NOTES Includes *Paluxysaurus jonesi*. May not be a brachiosaurid.

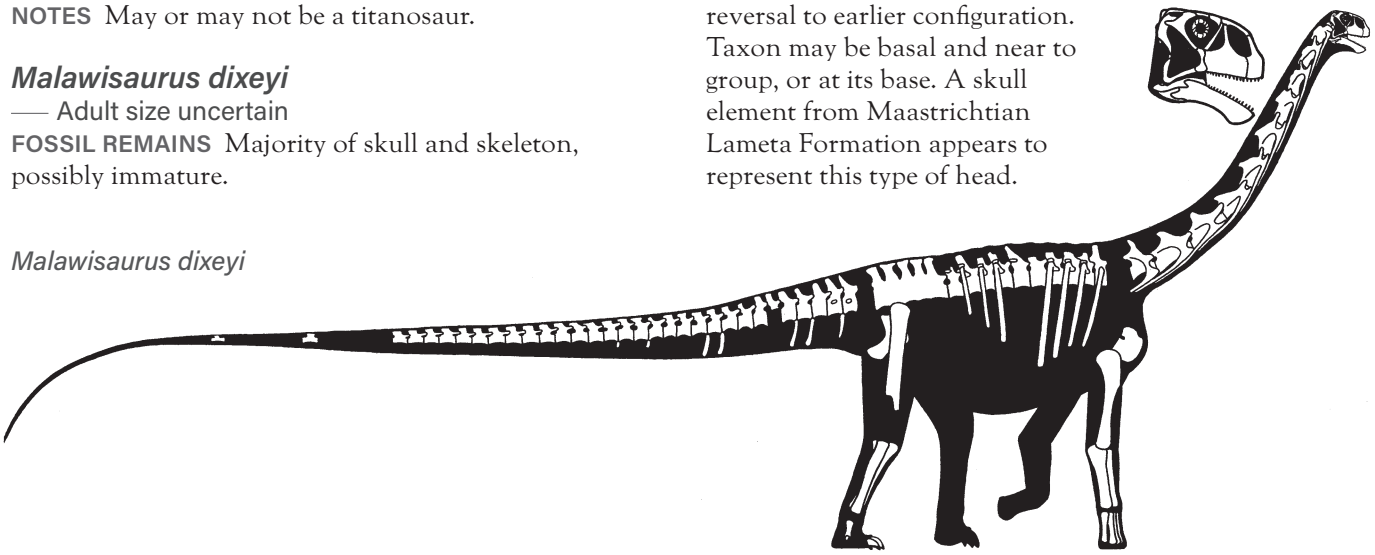
Europatitan eastwoodi
— 20 m (65 ft) TL, 25 tonnes
FOSSIL REMAINS Minority skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Barremian or early Aptian.
DISTRIBUTION AND FORMATION/S Spain; Castrillo de la Reina.
NOTES Inclusion of two enormous cervicals found near skeleton is incorrect because they are much too large for it.

— TITANOSAURIFORM MISCELLANEA

Liaoningotitan sinensis
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Lower jaw strongly downturned.
AGE Early Cretaceous, late Barremian or early Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China, Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES May or may not be a titanosaur.

Malawisaurus dixeyi
— Adult size uncertain
FOSSIL REMAINS Majority of skull and skeleton, possibly immature.
ANATOMICAL CHARACTERISTICS Head small, short, and deep; bony nostrils not retracted, lower jaw not short, teeth lining front half of jaws and pencil shaped. Neck broad, not elongated. Tail long and slender.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Malawi; unnamed formation.
NOTES Usual placement among titanosaurids problematic because of short head, although may be a partly juvenile feature, or a reversal to earlier configuration. Taxon may be basal and near to group, or at its base. A skull element from Maastrichtian Lameta Formation appears to represent this type of head.

Malawisaurus dixeyi

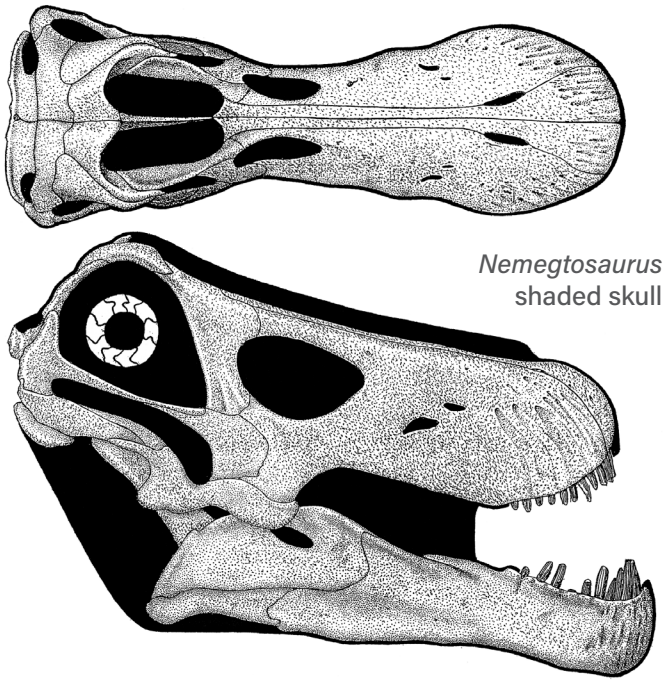


— TITANOSAURIDS

LARGE TO ENORMOUS TITANOSAURIFORMS OF THE CRETACEOUS UP TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads long, shallow; bony nostrils strongly retracted to above the orbits but fleshy nostrils probably still near front of snout, lower jaws short, shallow, pencil-shaped teeth limited to front of jaws, heads flexed downward relative to necks. Trunk vertebrae more flexible, possibly aiding rearing. Tails moderately long, very flexible especially upward, ending in a short whip. Arms at least fairly long, so shoulders as high as or higher than hips. Often armored, usually lightly especially in adults.
HABITS Often used armor as the passive side of their defense strategy, may have been most important in the more vulnerable juveniles. Flexible tails may have been used as display organs by arcing them over the back. Fossil dung indicates titanosaurs consumed flowering plants, including early grasses, as well as nonflowering plants.

NOTES Absence from Antarctica probably reflects lack of sufficient sampling. The last of the sauropod groups, titanosaurs are the only sauropods known to have survived into the late Late Cretaceous. Armor may have assisted them in surviving in a world of increasingly sophisticated and gigantic predators. The relationships of the numerous but often incompletely preserved titanosaurs are not well understood; the group is potentially splittable into a number of subdivisions. A 2 m (6.5 ft) long probable shank bone, since disintegrated, from the latest Cretaceous Kallamedu Formation in India labeled *Bruhathkayosaurus matleyi* suggests a titanosaur of 120–200 tonnes, in which case it may be the largest known animal species and indicates that supersized sauropods survived to the close of the dinosaur era.



Nemegtosaurus shaded skull

— BASO-TITANOSAURIDS

LARGE TO ENORMOUS TITANOSAURIDS OF THE CRETACEOUS UP TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

Sarmientosaurus musacchioi

— Adult size uncertain

FOSSIL REMAINS Skull and minority of skeleton, probably immature.

ANATOMICAL CHARACTERISTICS Head broad in top view, snout somewhat pointed, lower jaw not short, teeth in front half of upper jaw and fairly large.

AGE Late Cretaceous, late Cenomanian or Turonian.

DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.

HABITAT/S Seasonally wet, well-forested floodplain.

NOTES Head represents a basal titanosaur condition.

Dongyangosaurus sinensis

— 15 m (50 ft) TL, 7 tonnes

FOSSIL REMAINS Minority of skeleton.

ANATOMICAL CHARACTERISTICS Insufficient information.

AGE Late Cretaceous, Turonian or Coniacian.

DISTRIBUTION AND FORMATION/S Eastern China; Jinhua.

NOTES May not be a titanosaurid.

Malarguesaurus florenciae

— Adult size uncertain

FOSSIL REMAINS Minority of large juvenile skeleton.

ANATOMICAL CHARACTERISTICS Insufficient information.

AGE Late Cretaceous, late Turonian.

DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.

HABITAT/S Well-watered woodlands with short dry season.

Tapuiasaurus macedoi

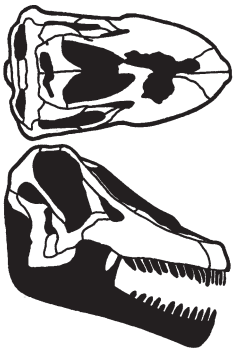
— Adult size uncertain

FOSSIL REMAINS Nearly complete skull and minority of skeleton.

ANATOMICAL CHARACTERISTICS Snout broad and rounded.

AGE Early Cretaceous, Aptian.

DISTRIBUTION AND FORMATION/S Southeastern Brazil; Quiricó.



Sarmientosaurus musacchioi immature

Tapuiasaurus macedoi

Gobititan shenzhouensis
— 20 m (65 ft) TL, 15 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.

Chubutisaurus insignis
— 18 m (60 ft) TL, 12 tonnes
FOSSIL REMAINS Two partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Cerro Barcino.

Austrosaurus mckillopi
— 20 m (65 ft) TL, 15 tonnes
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; Allaru.

Savannasaurus elliottorum
— 15 m (50 ft) TL, 7 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, latest Albian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; lower Winton.
HABITAT/S Well-watered, cold winters.

Diamantinasaurus matildae
— 27 m (90 ft) TL, 40 tonnes
FOSSIL REMAINS Minority of skull and four skeletons, adult and juvenile.
ANATOMICAL CHARACTERISTICS Fingers and thumb claw present.
AGE Late Cretaceous, late Cenomanian and/or early Turonian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; upper Winton.
HABITAT/S Well-watered, cold winters.
NOTES May include *Australotitan cooperensis*.

Andesaurus delgadoi
— 15 m (50 ft) TL, 6 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Candeleros.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Epachthosaurus sciuttoi
— 13 m (45 ft) TL, 5 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Some fingers present.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.

Aegyptosaurus baharijensis
— 15 m (50 ft) TL, 6 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Egypt; Bahariya.
HABITAT/S Coastal mangroves.

Atacamatitan chilensis
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Northern Chile; Tolar.

Choconsaurus baileywillisi
— 17 m (14 ft) TL, 10 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Hand elongated.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lower Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.

Baotianmansaurus henanensis
— 20 m (65 ft) TL, 15 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Eastern China; Gaogou.
NOTES Position within titanosaurs uncertain.

— COLOSSOSAURIANS/LITHOSTROTIANS

LARGE TO ENORMOUS TITANOSAURIDS OF THE LATE EARLY CRETACEOUS TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Necks short to long. Tails more flexible. Fingers and thumb claws absent. "Egg tooth" at tip of snout of hatchlings.
HABITS Dozens of spherical 0.15 m (6 in) eggs deposited in irregular shallow nests 1–1.5 m (3–5 ft) across. Nests were probably covered with vegetation that generated heat through fermentation, or they were placed near geothermal heat sources; nests formed large nesting areas. Parents probably abandoned nests.
NOTES The relative placement and contents of the two groups are highly different. The juvenile egg tooth is likely to have been a wider dinosaur feature. The last of the sauropods.

Elaltitan lilloi
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.

Rinconsaurus caudamirus
— 11 m (36 ft) TL, 2.5 tonnes
FOSSIL REMAINS Parts of several skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Cretaceous, Turonian or Coniacian.
DISTRIBUTION AND FORMATION/S Western Argentina; Rio Neuquén.
HABITAT/S Well-watered woodlands with short dry season.

Bonitasaura salgadoi
— 10 m (33 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Behind lower teeth a short, cutting beak appears to be present. Neck moderately long.
AGE Late Cretaceous, upper Santonian.
DISTRIBUTION AND FORMATION/S Central Argentina; upper Bajo de la Carpa.
HABITS Predominantly grazed ground cover, also able to rear to high browse. Appears to have complemented the cropping ability of its front teeth with a supplementary beak immediately behind.
NOTES Apparently the only beaked sauropod yet known. Other sauropods known to have had similarly broad, square, ground-grazing beaks were rebbachisaurid diplodocoids like *Nigersaurus*.

Muyelensaurus pecheni
— 11 m (36 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Lightly built.
AGE Late Cretaceous, late Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.
HABITAT/S Well-watered woodlands with short dry season.

Mendozasaurus neguyelap
— 20 m (65 ft) TL, 16 tonnes
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Neck fairly short. Vertebral spines very broad.
AGE Late Cretaceous, Turonian to Coniacian.
DISTRIBUTION AND FORMATION/S Western Argentina; Rio Neuquén.
HABITAT/S Well-watered woodlands with short dry season.

Ampelosaurus atacis
— 16 m (50 ft) TL, 8 tonnes
FOSSIL REMAINS Minority of a few skeletons.
ANATOMICAL CHARACTERISTICS Teeth broad, line most of length of dentary.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S France; Grès de Labarre, Marnes Rouges Inférieures, Grès de Saint-Chinian.
NOTES *Ampelosaurus* shows that broad-toothed sauropods survived until the last stage of the dinosaur era.

Jainosaurus septentrionalis
— 18 m (60 ft) TL, 11 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle to late Maastrichtian.
DISTRIBUTION AND FORMATION/S Central India; Lameta.
NOTES May be same genus as *Titanosaurus indicus*, which is based on inadequate remains.

Arrudatitan maximus
— 15 m (50 ft) TL, 6 tonnes
FOSSIL REMAINS Partial skeleton.

ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Adamantina.
HABITAT/S Semiarid.

Maxakalisaurus topai
— 13 m (45 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Cretaceous, probably Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Adamantina.

Aeolosaurus rionegrinus
— 14 m (45 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Angostura Colorada.

Gondwanatitan faustoi
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton, possibly immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Adamantina.

Adamantisaurus mezzalirai
— 13 m (43 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably Campanian or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Brazil; Adamantina.

Lirainosaurus astibiae
— Adult size uncertain
FOSSIL REMAINS Minority of several skeletons, possibly immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Northern Spain; unnamed formation.

Paralititan stromeri
— 27 m (90 ft) TL, 40 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Egypt; Bahariya.
HABITAT/S Coastal mangroves.
NOTES Early claims that *Paralititan* rivaled the largest titanosaurs in size were incorrect.

Laplatasaurus araukanicus
— 18 m (60 ft) TL, 11 tonnes
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Central Argentina; Allen.
HABITAT/S Semiarid coastline.

Pellegrinisaurus powelli
— 25 m (80 ft) TL, 30 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early or middle Campanian.
DISTRIBUTION AND FORMATION/S Central Argentina; upper Anacleto or lower Allen.
NOTES A problematically large number of Anacleto and lower Allen titanosaurs have been named; smaller examples including *Neuquensaurus*, *Barrosasaurus casamiquelai*, *Narambuenatitan palomoi*, *Pitekunsaurus macayai*, and *Overosaurus paradasorum* may have been juveniles of other titanosaurs from this formation. At least one of the known species may have laid the numerous eggs found in this formation.

Antarctosaurus wichmannianus
— 17 m (55 ft) TL, 10 tonnes
FOSSIL REMAINS Minority of skull? And skeleton.
ANATOMICAL CHARACTERISTICS Front of snout broad and squared off.
AGE Late Cretaceous, late Santonian or early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; Anacleto, level uncertain.
HABITAT/S Seasonally semiarid.
HABITS Jaws adapted to browse swaths of plant material, perhaps at ground level.

Rapetosaurus krausei
— Adult size uncertain
FOSSIL REMAINS Majority of skulls and a skeleton, large juvenile.
ANATOMICAL CHARACTERISTICS Snout broad and rounded, head hourglass shaped in top view. Neck long.
AGE Late Cretaceous, Campanian.

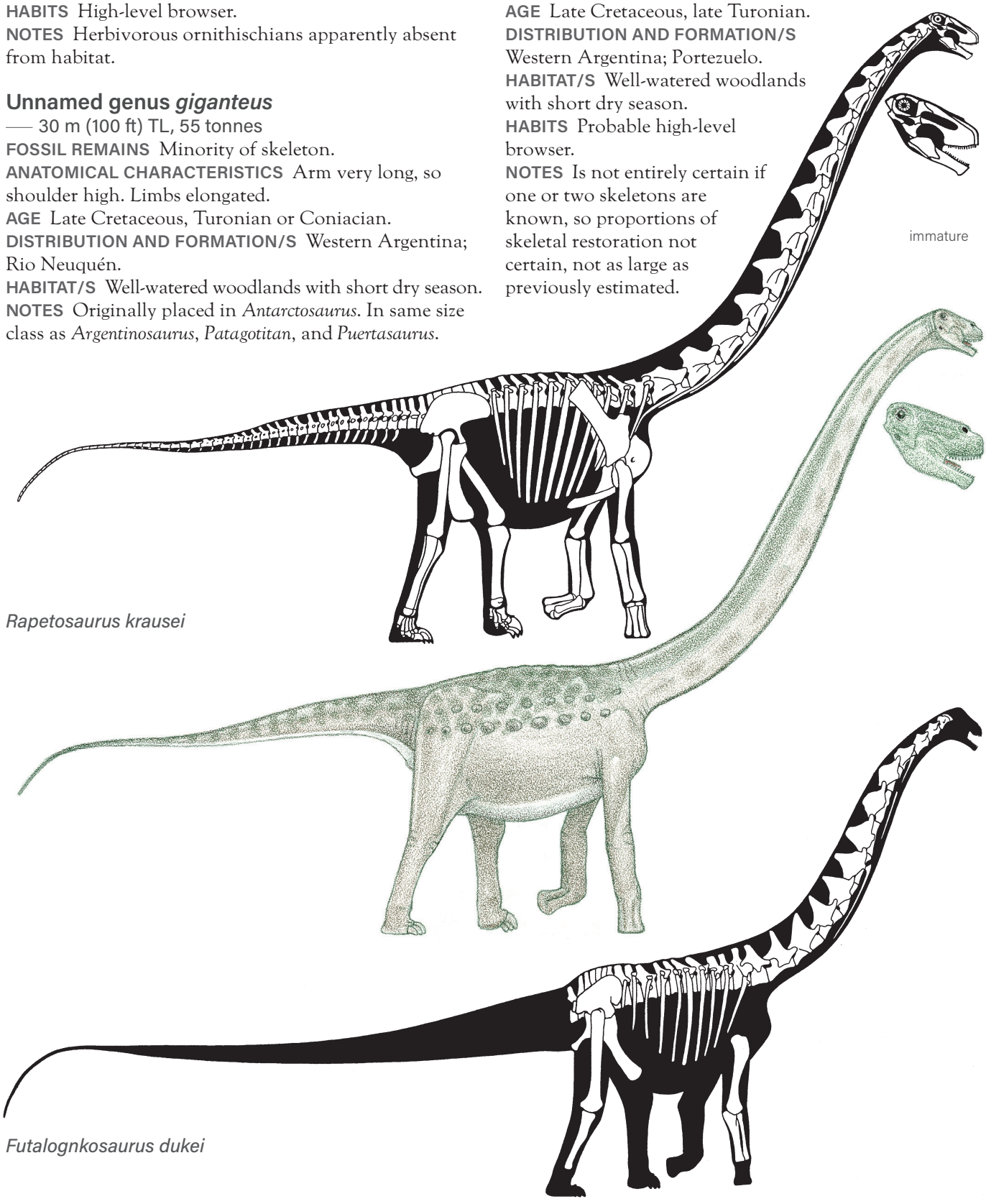
DISTRIBUTION AND FORMATION/S Madagascar; Maevarano.
HABITAT/S Seasonally dry floodplain with coastal swamps and marshes.
HABITS High-level browser.
NOTES Herbivorous ornithischians apparently absent from habitat.

Unnamed genus *giganteus*

— 30 m (100 ft) TL, 55 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Arm very long, so shoulder high. Limbs elongated.
AGE Late Cretaceous, Turonian or Coniacian.
DISTRIBUTION AND FORMATION/S Western Argentina; Rio Neuquén.
HABITAT/S Well-watered woodlands with short dry season.
NOTES Originally placed in *Antarctosaurus*. In same size class as *Argentinosaurus*, *Patagotitan*, and *Puertasaurus*.

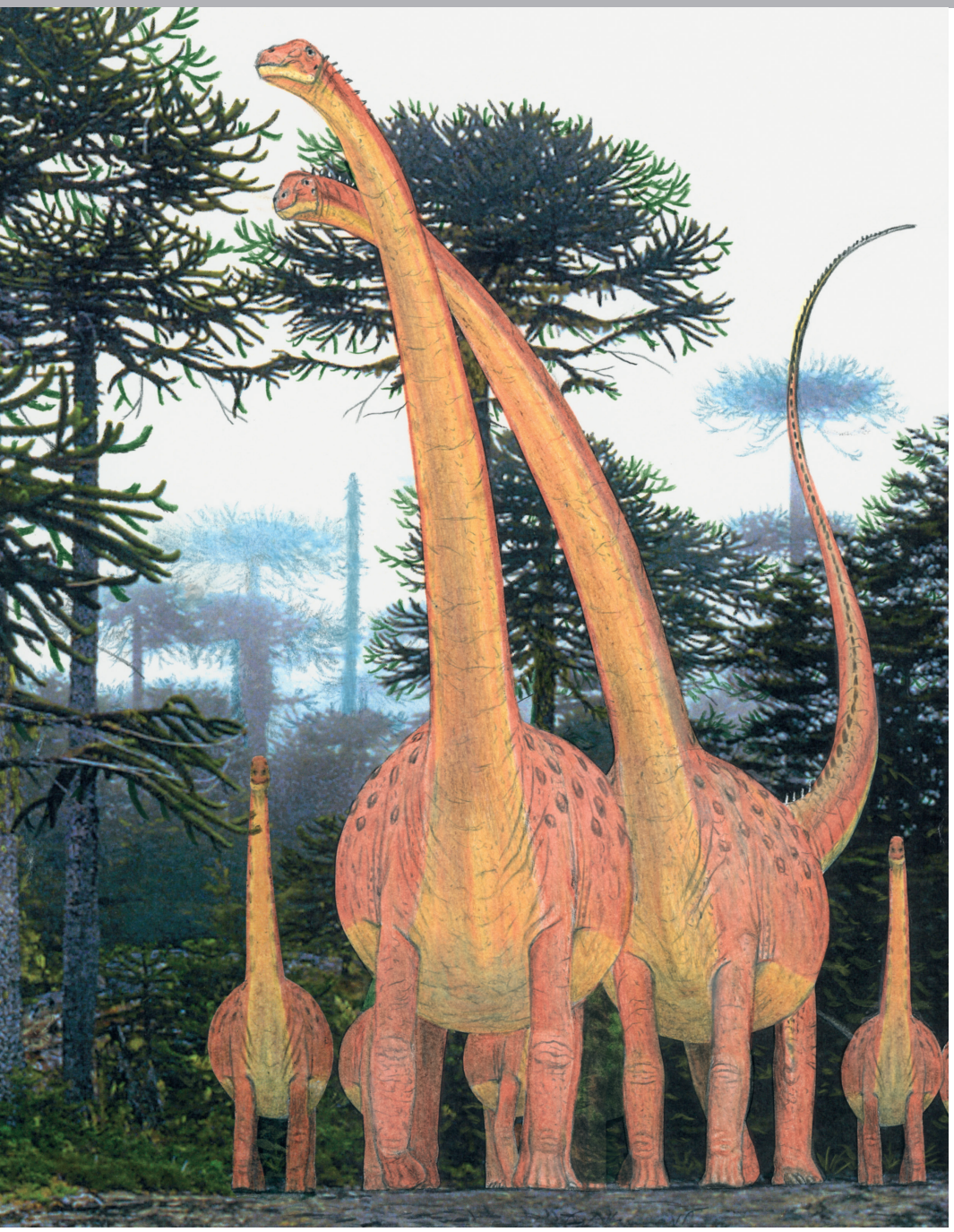
Futalognkosaurus dukei

— 24 m (80 ft) TL, 29.5 tonnes
FOSSIL REMAINS Majority of skeleton(s).
ANATOMICAL CHARACTERISTICS Neck long.
AGE Late Cretaceous, late Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.
HABITAT/S Well-watered woodlands with short dry season.
HABITS Probable high-level browser.
NOTES Is not entirely certain if one or two skeletons are known, so proportions of skeletal restoration not certain, not as large as previously estimated.



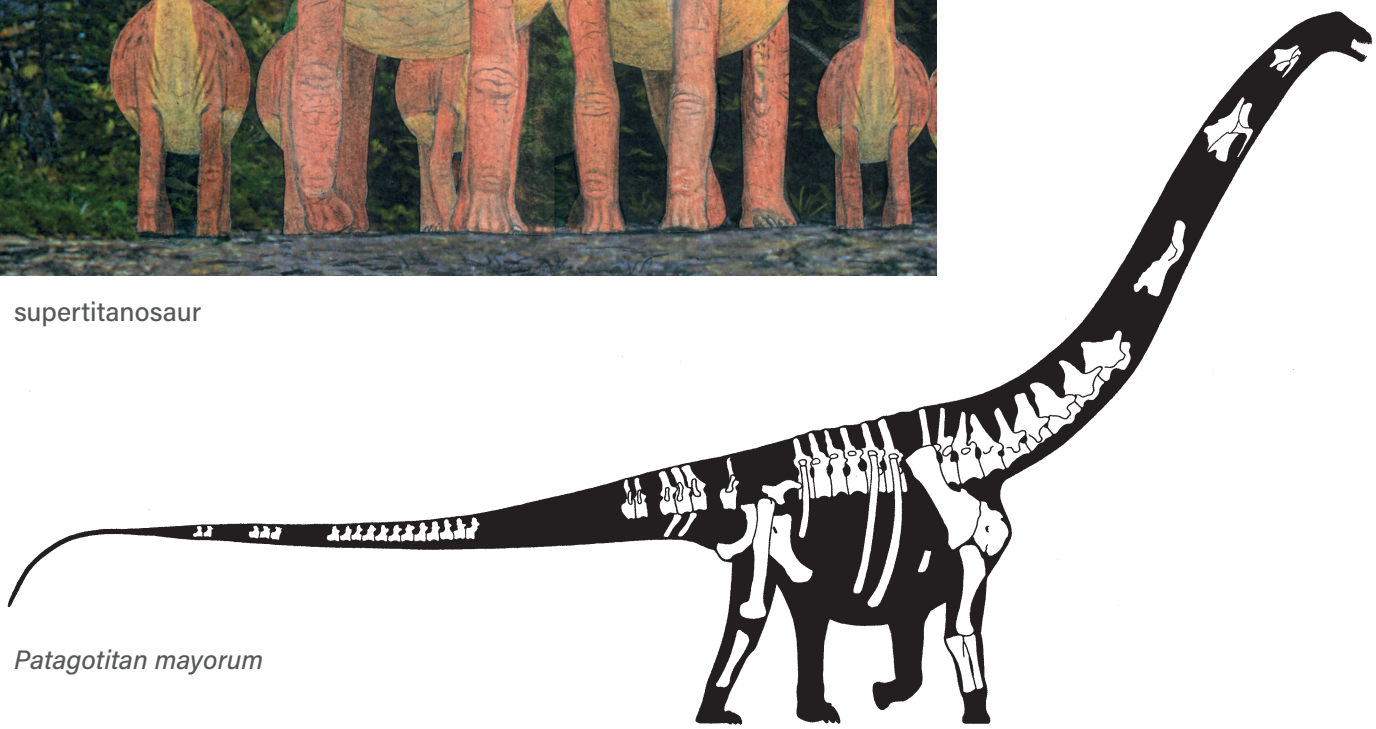
Rapetosaurus krausei

Futalognkosaurus dukei



supertitanosaur

Patagotitan mayorum
31 m (100 ft) TL, 57 tonnes
FOSSIL REMAINS Some partial skeletons.
ANATOMICAL CHARACTERISTICS Neck long. Shoulder moderately high.
AGE Early Cretaceous, latest Albian.
DISTRIBUTION AND FORMATION/S Southern Argentina; middle Cerro Barcino.
HABITAT/S Seasonally very dry.
NOTES Some mass estimates have been excessive, largest land animal represented by most of skeleton, those remains have allowed the size of other titanosaurus to be better restored and estimated.



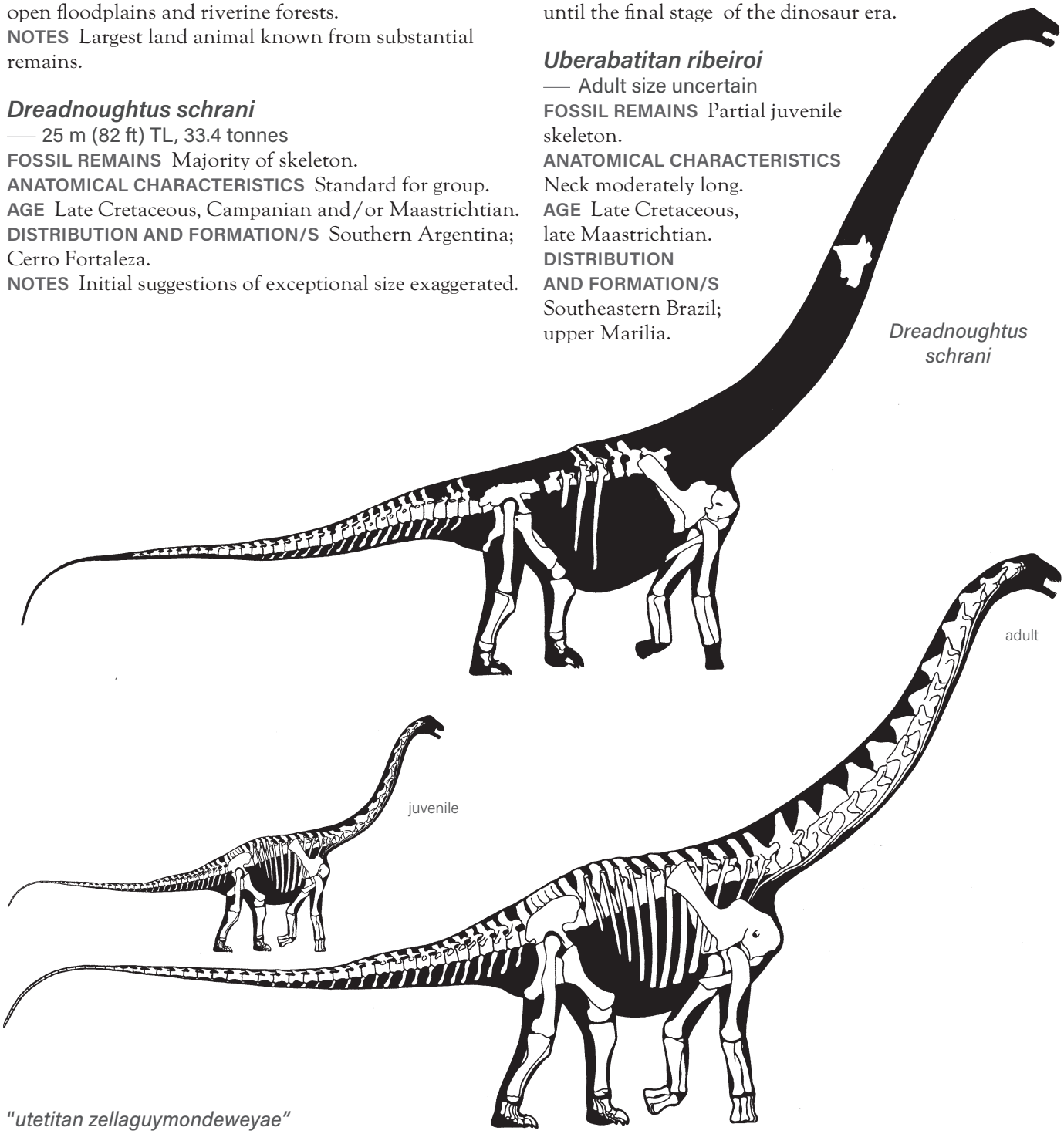
Patagotitan mayorum

Argentinosaurus huinculensis
— 35 m (115 ft) TL, 80 tonnes
FOSSIL REMAINS Minority of skeleton and some other elements.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian.
DISTRIBUTION AND FORMATION/S Western Argentina; lowermost upper Huincul.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
NOTES Largest land animal known from substantial remains.

Dreadnoughtus schrani
— 25 m (82 ft) TL, 33.4 tonnes
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, Campanian and/or Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Cerro Fortaleza.
NOTES Initial suggestions of exceptional size exaggerated.

Puertasaurus reuili
— 30 m (100 ft) TL, 65 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Pari Aike.
HABITAT/S Short wet season, otherwise semiarid with open floodplains and riverine forests.
NOTES Indicates that supersized sauropods survived until the final stage of the dinosaur era.

Uberabatitan ribeiroi
— Adult size uncertain
FOSSIL REMAINS Partial juvenile skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; upper Marilia.



Baurutitan britoi
— Adult size uncertain
FOSSIL REMAINS Three partial skeletons, immature.
ANATOMICAL CHARACTERISTICS Neck long.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern Brazil; lower Serra da Galga.
NOTES Probably includes *Trigonosaurus pricei*.

Alamosaurus sanjuanensis?
— 25 m (80 ft) TL, 30 tonnes
FOSSIL REMAINS Possibly a few bones of several individuals.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S New Mexico; lower Ojo Alamo.
NOTES Original fossil is one bone, and others are also not highly distinctive, so status of taxon problematic. A substantial number of partial fossils assigned to this taxon from US Southwest from the late Campanian to late Maastrichtian are very unlikely to represent one species or even genus. These titanosaurs represent a reinhabitation of southwestern North America by sauropods from South America or less probably Asia after a sauropod hiatus over most of the Late Cretaceous.

"utetitan zellaguymondeweyae"
— 20 m (65 ft) TL, 20 tonnes
FOSSIL REMAINS Partial skeleton, other possible remains, immature to juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Utah, Texas?; lower North Horn, upper Black Peaks?
NOTES Usually and incorrectly placed in much earlier *Alamosaurus*. Contemporary fossils from Texas may or may not belong to taxon.

— SALTASAURS

MEDIUM-SIZED COLLOSSOSAURIANS/LITHOSTROTIANS OF THE LATE CRETACEOUS OF EURASIA AND SOUTH AMERICA.

ANATOMICAL CHARACTERISTICS Uniform. Necks short by sauropod standards.

Isisaurus colberti
— 18 m (60 ft) TL, 15 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Neck moderately long. Arm and hand very long, so shoulder much higher than hip.
AGE Late Cretaceous, Maastrichtian.
DISTRIBUTION AND FORMATION/S Central India; Lameta.
NOTES Approaches brachiosaurs in its giraffe-like form.

Magyarosaurus dacus or *Paludititan nalatzensis*
— 6 m (20 ft), 1 tonne
FOSSIL REMAINS A dozen partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Romania; Sânpetru.
HABITAT/S Forested island.
NOTES Whether the remains represent one or more taxa, and which has priority, await further research. Small size of most individuals implies island dwarfism, but some researchers cite larger sauropod fossils and higher estimate of size of island as contrary evidence.

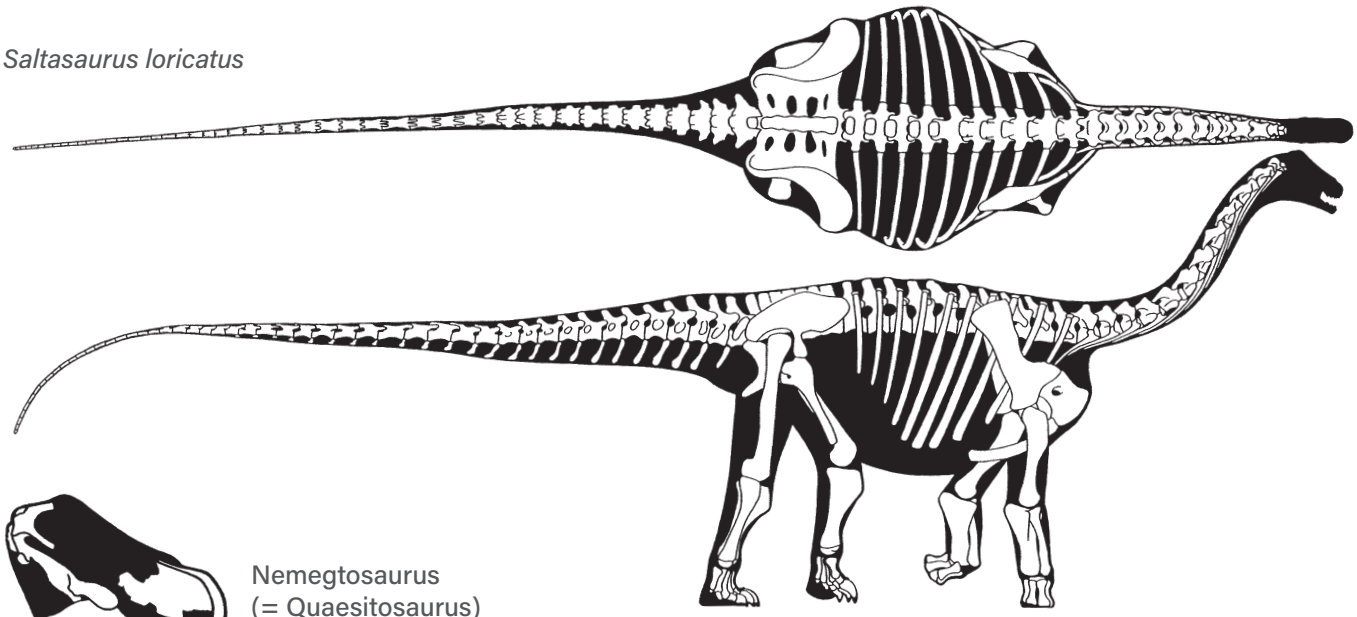
Saltasaurus (= *Neuquensaurus*) *australis*
— 7.5 m (24 ft) TL, 1.8 tonnes
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; upper Anacleto.
HABITAT/S Seasonally semiarid.
NOTES May include *Microcoelus patagonicus* juveniles.

Saltasaurus robustus
— 8 m (25 ft) TL, 2 tonnes
FOSSIL REMAINS A few partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Central Argentina; Allen.
HABITAT/S Semiarid coastal.
NOTES May be direct ancestor of *S. loricatus*.

Saltasaurus loricatus (see p.260)
— 8.5 m (27 ft) TL, 2.6 tonnes
FOSSIL REMAINS Minority of skull and half a dozen partial skeletons.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, probably early Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Lecho.

Nemegtosaurus (= *Quaesitosaurus*) *orientalis* (see p.260)
— Adult size uncertain
FOSSIL REMAINS Partial skull.

Saltasaurus loricatus



Nemegtosaurus
(= Quaesitosaurus)
orientalis

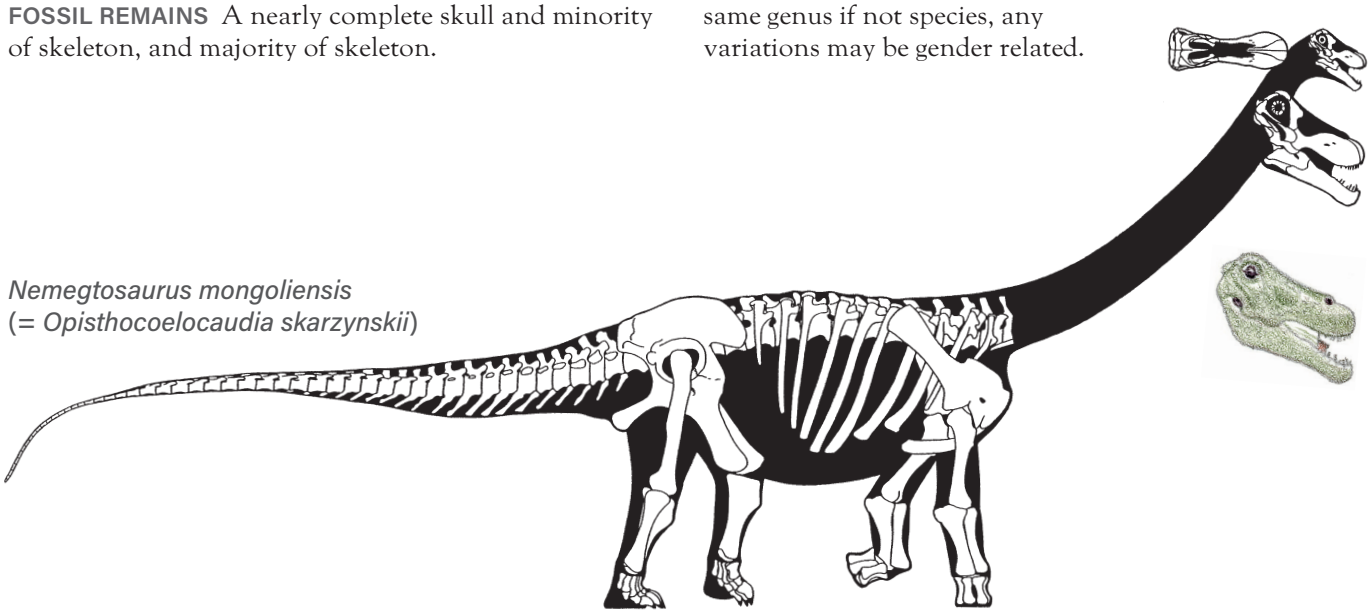
ANATOMICAL CHARACTERISTICS Head standard for group.
AGE Late Cretaceous, latest Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.
HABITS Fed on vegetation along streams and oases.
NOTES Shows that this sauropod dwelled in a desert, as do some elephants. May be direct ancestor of *N.mongoliensis*.

Nemegtosaurus mongoliensis (= *Opisthocoelicaudia skarzynskii*)

— 13+ m (43+ ft) TL, 9.5 tonnes
FOSSIL REMAINS A nearly complete skull and minority of skeleton, and majority of skeleton.

ANATOMICAL CHARACTERISTICS Snout broad and rounded, head strongly midconstricted, hourglass shaped in top view. Skeleton massively constructed. Shoulder same height as hip. Hand broad.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
NOTES *Nemegtosaurus* and *Opisthocoelicaudia* are often considered entirely different sauropods, but both are titanosaurs with only minor differences from the same level of the Nemegt, so are probably same genus if not species, any variations may be gender related.

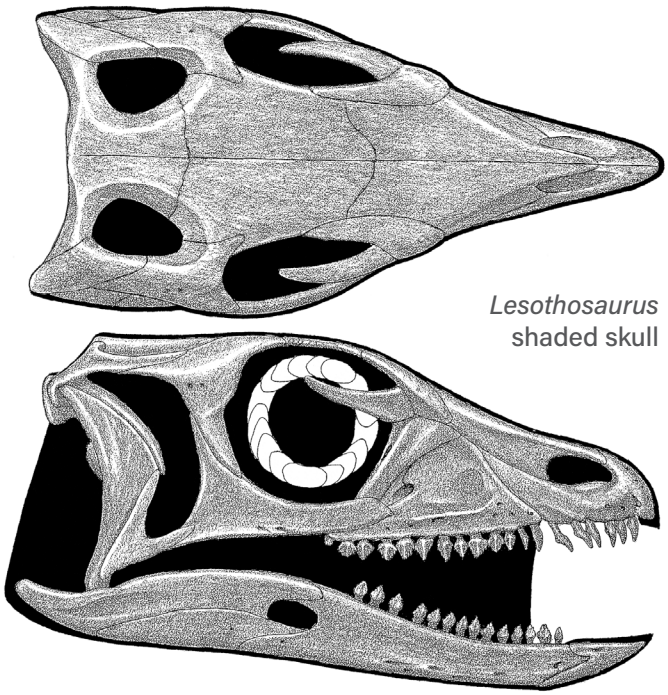
Nemegtosaurus mongoliensis
(= *Opisthocoelocaudia skarzynskii*)



ORNITHISCHIANS

SMALL TO GIGANTIC HERBIVOROUS DINOSAURS FROM THE LATE TRIASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Extremely variable. Head size and shape variable, skulls heavily built, beaks at front of jaws, anchored on toothless predentary bone on lower jaws, vertical coronoid projection at back end of lower tooth row increased leverage of jaw muscles, rows of leaf-shaped teeth covered by presumably elastic cheeks, jaw gap limited. Necks not long, ribs so short they do not overlap, increasing cervical flexibility of necks when long. Trunks stiff. Tails short to moderately long. Bipedal to quadrupedal. Arms short to long, usually five fingers, sometimes four or three. Pubes strongly retroverted to accommodate large bellies, pelves large, ilia shallow. Usually four toes, sometimes three. Skeletons not pneumatic, birdlike respiratory system not present. Brains reptilian in size and form.
HABITAT Very variable, from sea level to highlands, from tropics to polar winters, from arid to wet.
HABITS Predominantly herbivorous browsers and grazers, although smaller examples may have been prone to pick up and consume small animals, and others may have scavenged; extensively chewed food before swallowing. Defense ranged from passive armor to running to aggressive combat. Smaller species potentially or actually able to burrow.



Lesothosaurus shaded skull

BASO-ORNITHISCHIANS

SMALL ORNITHISCHIANS LIMITED TO THE LATE TRIASSIC AND EARLY JURASSIC OF SOUTH AMERICA AND AFRICA.

ANATOMICAL CHARACTERISTICS Heads modest sized, subtriangular, beaks narrow and not hooked, teeth under upper beak, main tooth rows not deeply inset, large eyes shaded by overhanging rim. Tails moderately long, stiffened by ossified tendons. Bipedal except could move quadrupedally at slow speeds. Arms fairly short, hands small, five grasping fingers tipped with small blunt claws. Legs long, flexed, and gracile so speed potential high, four long toes tipped with blunt claws. Competent surface swimmers, some diving ability.
HABITS Low-level browsers, picked up insects and small vertebrates. Predominantly terrestrial, probably some climbing ability. Main defense high speed.
NOTES Closest living analogues small kangaroos, deer, and antelope. The relationships of these generalized ornithischians are uncertain, ultimately splittable into a number of divisions; some may belong to other groups. Absence from other continents may reflect lack of sufficient sampling.

Pisanosaurus mertii

— 1.3 m (4.5 ft) TL, 5 kg (10 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Triassic, late Carnian.
DISTRIBUTION AND FORMATION/S Northern Argentina; Ischigualasto.
HABITAT/S Seasonally well-watered forests, including dense stands of giant conifers.
NOTES Generally considered the earliest known ornithischian, or may be a silesaurid protodinosaur, or silesaurids may be basal ornithischians.

Eocursor parvus

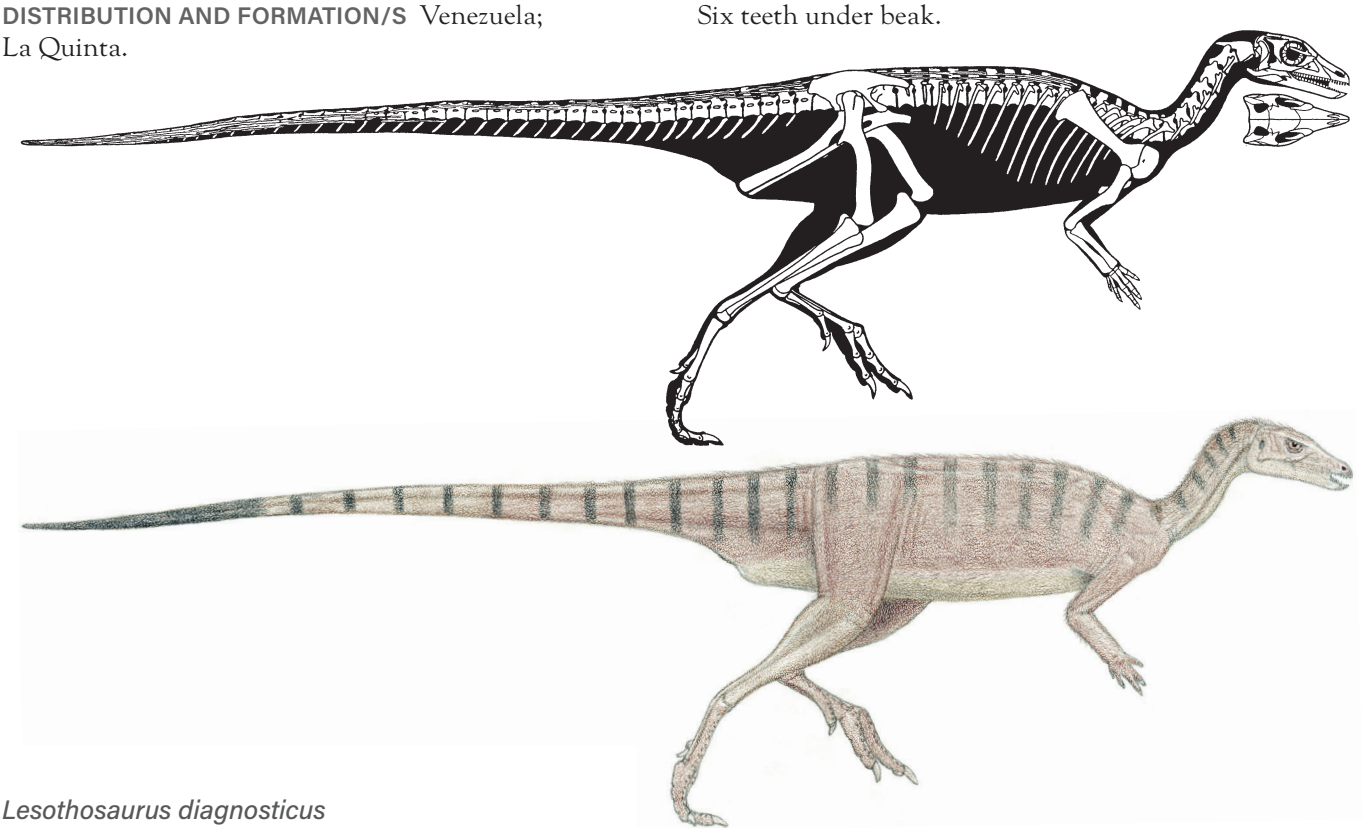
— 1 m (3.5 ft) TL, 2.5 kg (5 lb)
FOSSIL REMAINS Partial skull and skeleton, large juvenile.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Triassic, Rhaetian.
DISTRIBUTION AND FORMATION/S South Africa; lower Elliot.
HABITAT/S Arid.

Laquintasaura venezuelae

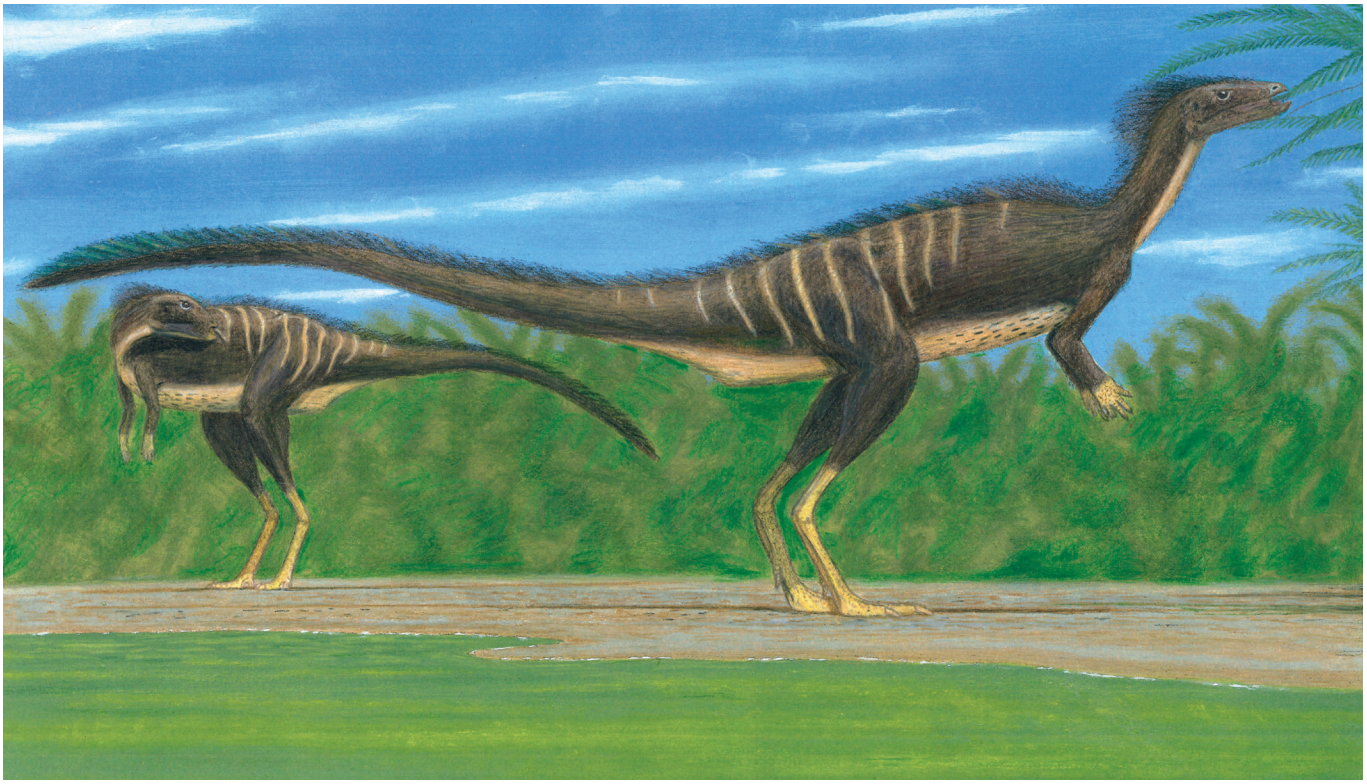
— 1 m (3 ft) TL, 2 kg (4 lb)
FOSSIL REMAINS Bone bed.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Jurassic, early Hettangian.
DISTRIBUTION AND FORMATION/S Venezuela; La Quinta.

Lesothosaurus diagnosticus

— 2 m (6.5 ft) TL, 18 kg (40 lb)
FOSSIL REMAINS Majority of some skulls and skeletons, juvenile to adult.
ANATOMICAL CHARACTERISTICS Six teeth under beak.



Lesothosaurus diagnosticus



AGE Early Jurassic, late Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.

NOTES Originally known as *Fabrosaurus australis* based on inadequate remains; *Stormbergia dangershoeki* probably the adult of this species. May be a genasaur, possibly thyreophoran.

GENASAURS

SMALL TO GIGANTIC ORNITHISCHIANS FROM THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Main tooth rows deeply inset, enlarging capacity of cheek spaces.
HABITAT/S Very variable, from sea level to highlands, from tropics to polar winters, from arid to wet.

— THYREOPHORANS

SMALL TO VERY LARGE ARMORED GENASAUR ORNITHISCHIANS FROM THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Variable. Heads not large, solidly constructed, eyes not large. Skeletons heavily built. Tails moderately long. Bipedal to fully quadrupedal, able to rear on hind legs. Arms short to long, five fingers. Four to three toes. Substantial armor always present, dense pavement of ossicles under throat in at least some examples.
ONTOGENY Growth apparently slower than in most dinosaurs.
HABITAT/S Very variable, from deserts to well-watered forests.
HABITS Low-level browsers and grazers. Generally not fast moving. Main defense passive armor, some may have used armor spines and clubs as weapons. Armored, heavy-boned bodies too dense for surface swimming, bottom walkers like hippos, ability to cross large bodies of water correspondingly limited.
NOTES *Lesothosaurus* may be at base of group. The only known armored ornithischians, among saurischians armor paralleled only by titanosaurs.

— SCELIDOSAURS

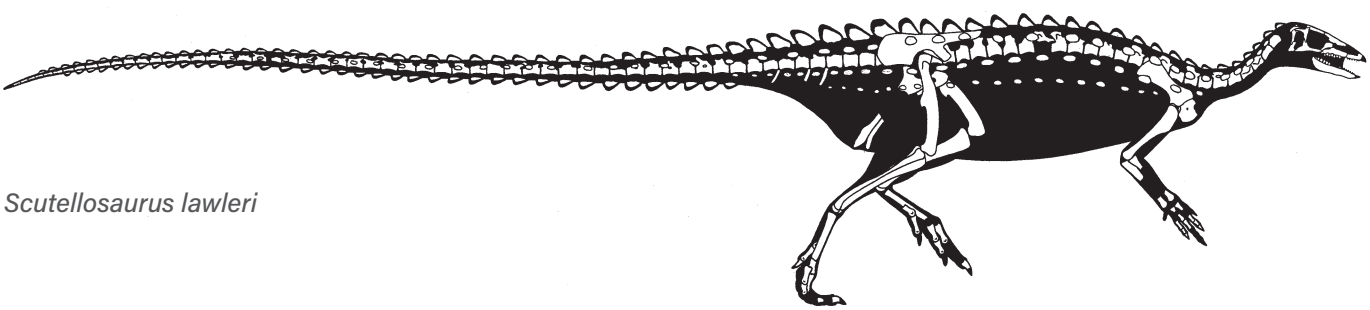
SMALL TO MEDIUM-SIZED THYREOPHORANS LIMITED TO THE EARLY JURASSIC OF EUROPE AND AFRICA.

ANATOMICAL CHARACTERISTICS Heads not large, solidly constructed, beaks narrow, eyes not large, teeth under upper beak. Bellies and hips moderately broad. Tails long. Bipedal to fully quadrupedal, arms and legs flexed so could run. Arms short to long, five fingers tipped with blunt claws. Four long toes tipped with blunt claws. Armor substantial but simple, generally scutes set in long rows, including top of vertebral series and bottom of tail.
HABITS Low-level browsers.
NOTES Members not certain. Absence from other continents probably reflects lack of sufficient sampling. May be splittable into a larger number of divisions or subdivisions.

Scutellosaurus lawleri

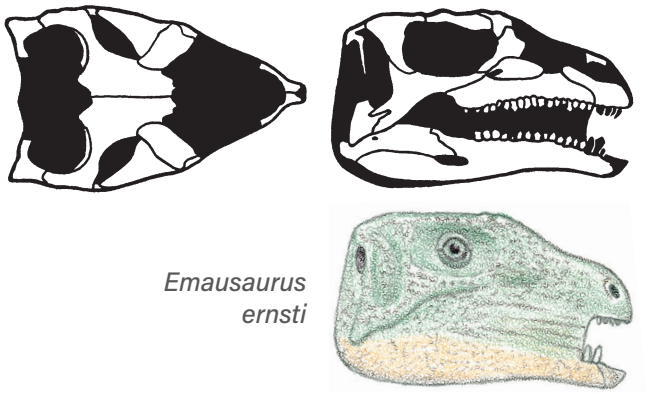
— 1.6 m (3.5 ft) TL, 5.6 kg (12 lb)
FOSSIL REMAINS Majority of a skull and a skeleton, partial skulls and skeletons, loose armor.

ANATOMICAL CHARACTERISTICS Head fairly shallow and narrow, snout pointed, six teeth under upper beak. Tail quite long. Arm too short to move quadrupedally except at low speeds. Leg fairly long, upper foot particularly so.



Scutellosaurus lawleri

AGE Early Jurassic, Sinemurian or Pliensbachian.
DISTRIBUTION AND FORMATION/S Arizona; middle Kayenta.
HABITAT/S Semiarid.
HABITS Largely bipedal, defense included running.
NOTES Only certain thyreophoran known to be strongly bipedal and have a very long tail; distribution of armor uncertain.



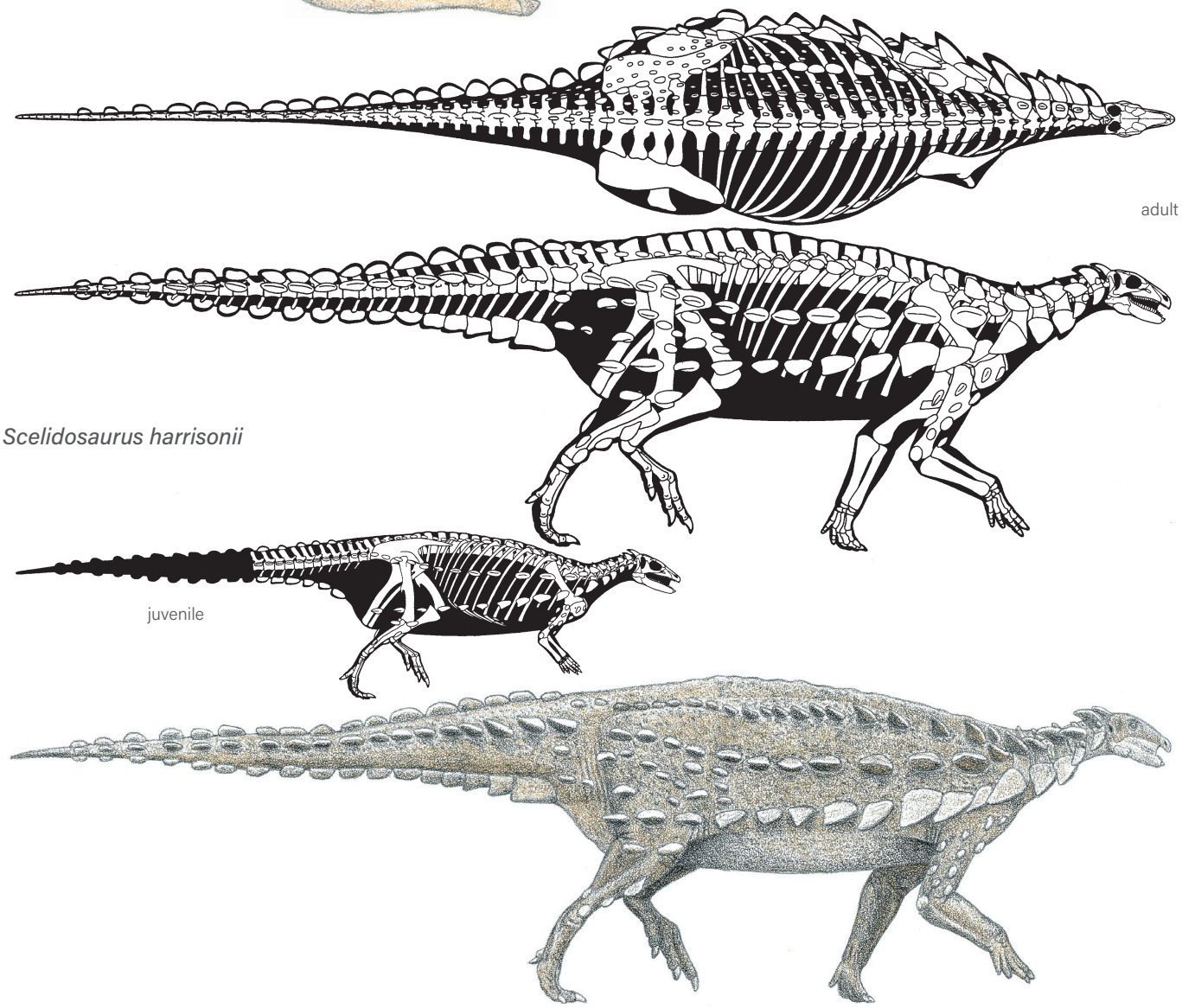
Emausaurus ernsti

Emausaurus ernsti

— 1.7 m (8 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head broad, snout sharply pointed in top view, four teeth under upper beak.
AGE Early Jurassic, Toarcian.
DISTRIBUTION AND FORMATION/S Germany; unnamed formation.

Scelidosaurus harrisonii

— 3.7 m (12 ft) TL, 320 kg (700 lb)
FOSSIL REMAINS Two complete skulls and a few skeletons, juvenile to adult, some with armor in place.
ANATOMICAL CHARACTERISTICS Head small, fairly narrow, a prominent hornlet adorns upper rim of back of skull on each side, five teeth under upper beak. Trunk and hips moderately broad. Adult arm long, so fully quadrupedal, juvenile arm relatively shorter so more



bipedal. Armor well developed but does not form a contiguous pavement.
AGE Early Jurassic, late Sinemurian.
DISTRIBUTION AND FORMATION/S Southwestern England; lower Lias.
NOTES Adult skeleton restored here is the first complete dinosaur fossil discovered; past restorations have been made obsolete by new description of remains. Some consider this the earliest basal ankylosaur.

— THYREOPHORAN MISCELLANEA

Jakapil kaniukura
— 1.5 m (5 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Lower jaw very deep at midlength, apparently no teeth under upper beak.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Candeleros.
NOTES May not be a thyreophoran.

— EURYPODS

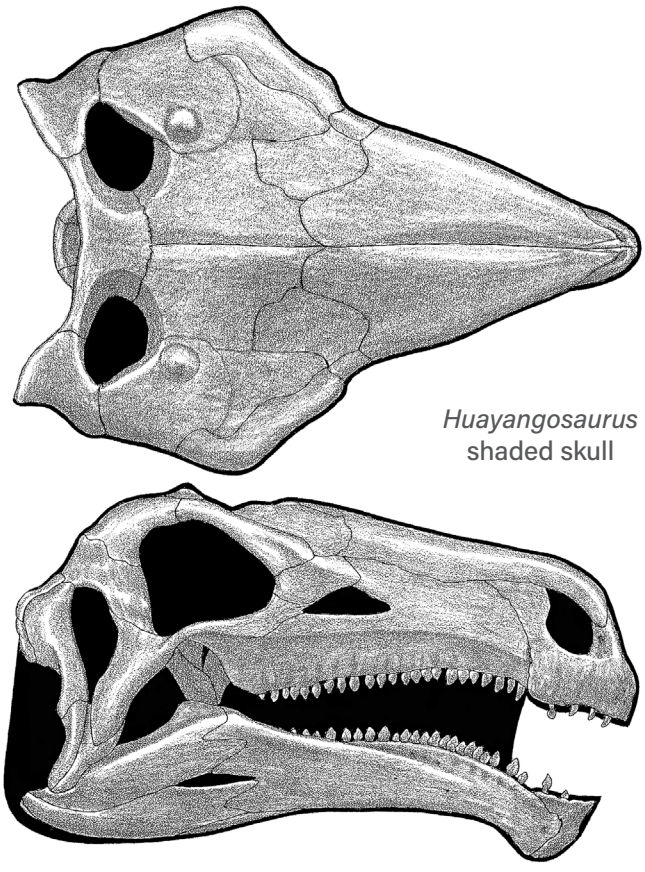
MEDIUM-SIZED TO VERY LARGE THYREOPHORANS FROM THE MIDDLE JURASSIC TO THE LATE CRETACEOUS OF NORTH AMERICA, EURASIA, AND AFRICA.

ANATOMICAL CHARACTERISTICS Teeth small. Hand, fingers, foot, and toes short, limiting speed, fingers and toes tipped with hooves.
ENERGETICS Energy levels and food consumption probably low for dinosaurs.

— STEGOSAURS

MEDIUM-SIZED TO VERY LARGE THYREOPHORANS FROM THE MIDDLE JURASSIC TO THE EARLY CRETACEOUS, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Beaks narrow. Necks U-curved. Tails moderately long. Largely quadrupedal, but may have often moved bipedally, especially when arms were much shorter than legs. Feet and three toes short, limiting speed. Armor predominantly parallel rows of tall plates and spikes running atop vertebral column.
HABITAT/S Semiarid to well-watered forests.
HABITS Low- to medium-level browsers. Main defense swinging tails to puncture flanks of theropods with spine arrays. In addition to protection, plates and spikes also for display, possibly thermoregulation.
NOTES Absence from some other continents may reflect insufficient sampling.



Huayangosaurus
shaded skull

— STEGOSAUR MISCELLANEA

Bashanosaurus primitivus
— Adult size uncertain
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
NOTES Either most basal known stegosaur or basal to group.

— HUAYANGOSAURIDS

MEDIUM-SIZED STEGOSAURS LIMITED TO THE MIDDLE JURASSIC OF ASIA.

ANATOMICAL CHARACTERISTICS Heads fairly deep, broad, teeth under upper beak. Bellies and hips moderately broad.

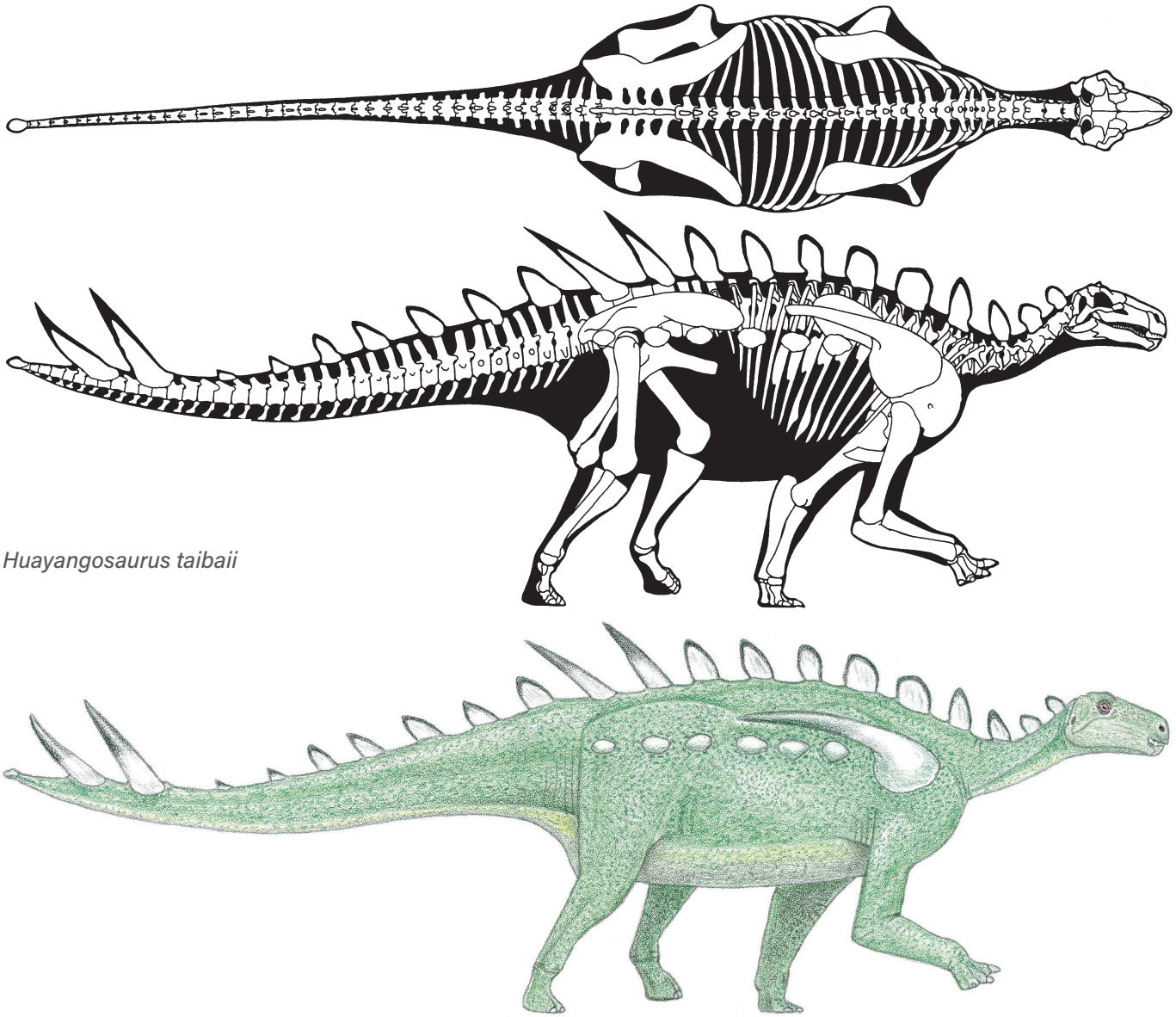
Arms moderately long, so shoulders as high as hips. Arms and legs flexed, so able to run.
HABITS Low-level browsers. Defense included running while swinging tails.

Isaberrysaura mollensis
— 5 m (15 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull and partial skeleton, gut contents.
ANATOMICAL CHARACTERISTICS Head very shallow, narrow, lower jaw fairly deep.
AGE Middle Jurassic, early Bajocian.

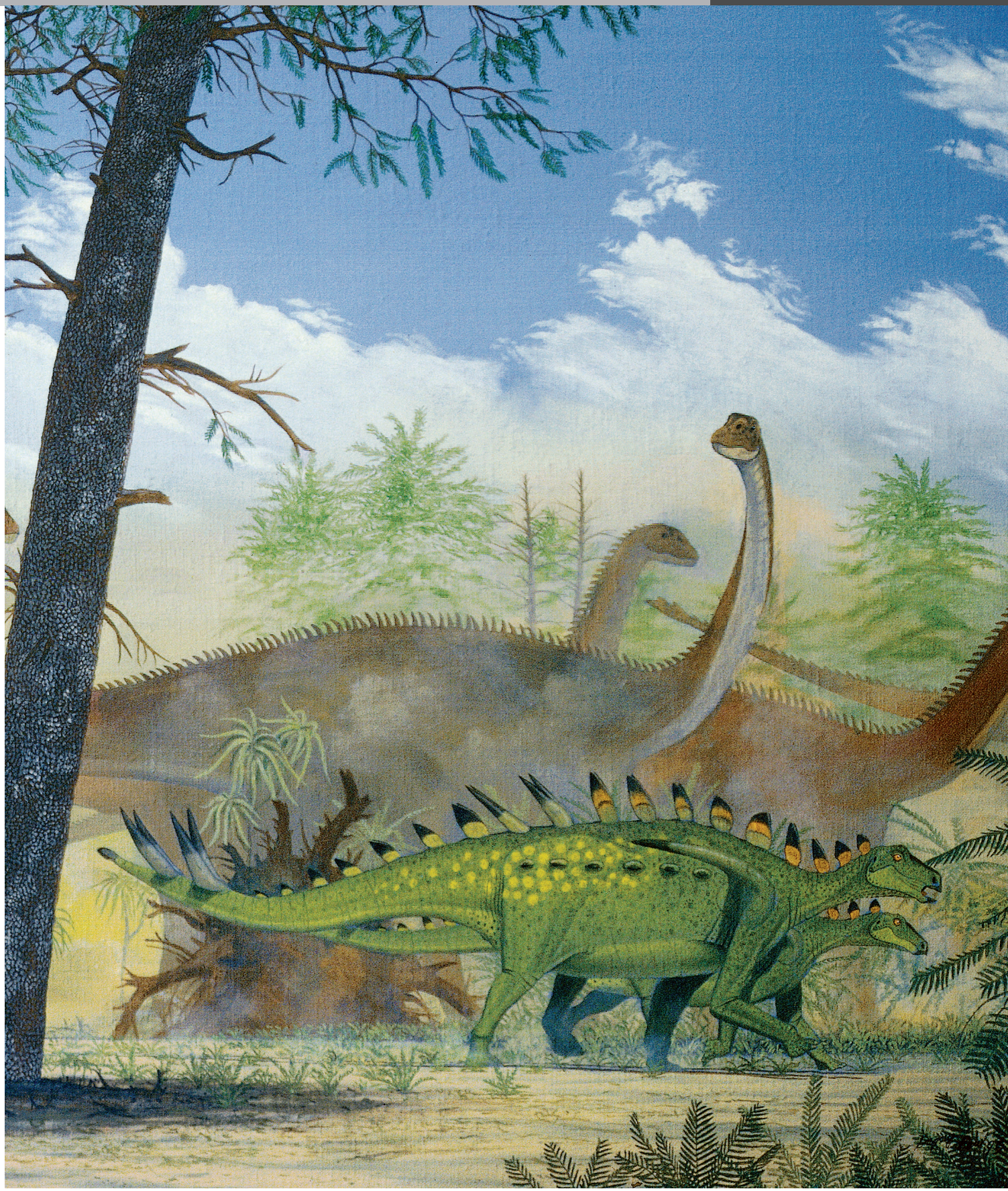
Isaberrysaura mollensis

DISTRIBUTION AND FORMATION/S Southern Argentina; upper Los Molles.
HABITAT/S Coastal.
HABITS Diet included cycad seeds.
NOTES Overall configuration of undescribed body uncertain.

Huayangosaurus taibaii
— 4 m (13 ft) TL, 540 kg (1,200 lb)
FOSSIL REMAINS Complete skull and skeleton and partial skeletons.
ANATOMICAL CHARACTERISTICS Head broad, snout narrow in top view, four teeth under upper beak. Long spine on shoulder, small club at tip of tail.
AGE Middle Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.



Huayangosaurus taibaii

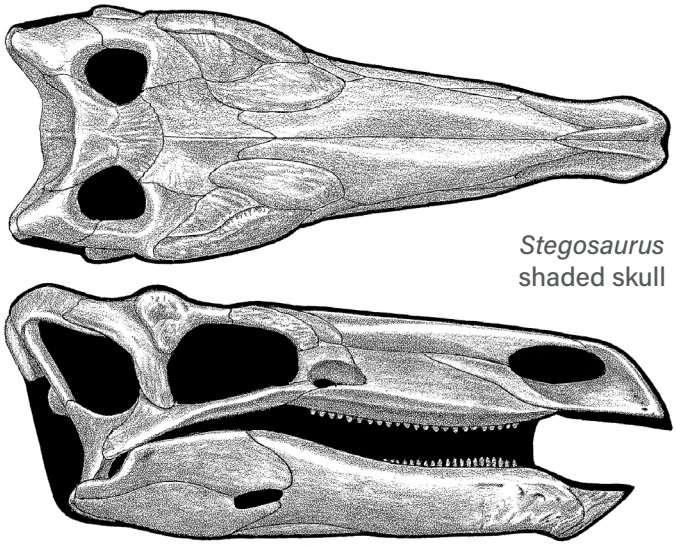


Huayangosaurus taibaii

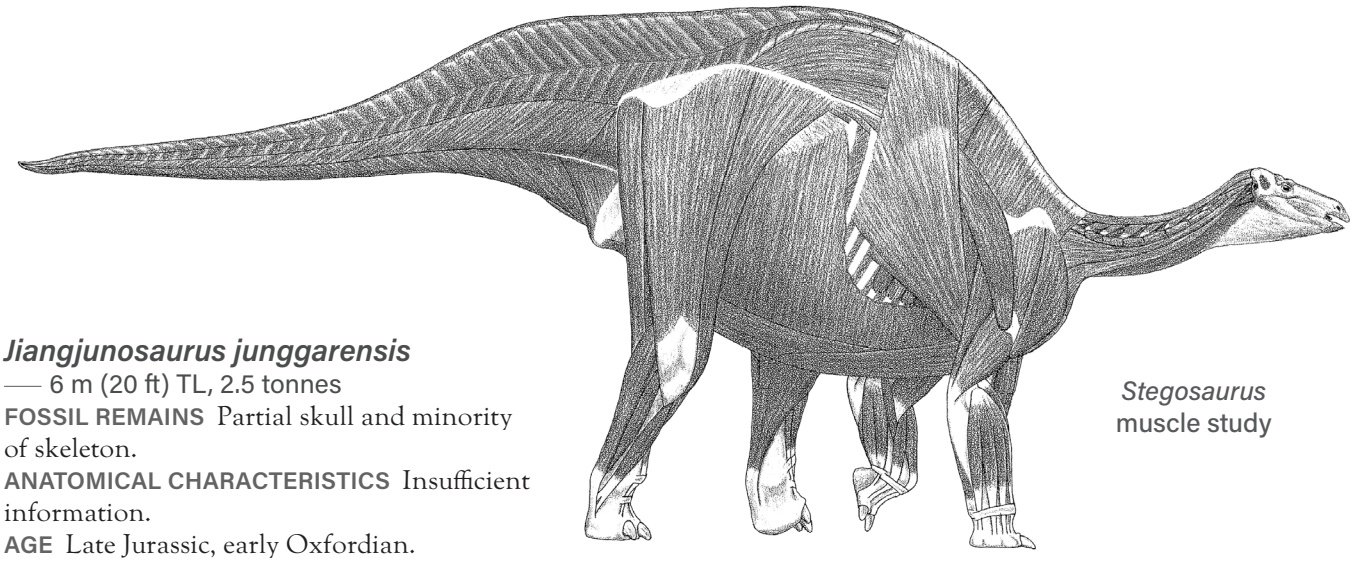
— STEGOSAURIDS

LARGE STEGOSAURS LIMITED TO THE LATE JURASSIC AND EARLY CRETACEOUS, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads small, slender, no teeth under upper beaks, teeth smaller. Necks slender. Trunk vertebral series downcurved, and arms fairly short, so shoulders lower than hips. Tails held high above ground. Arms and legs columnar and massively built, so not able to achieve a full run faster than elephants. Short arms, large hips, and stout tails with sled-shaped chevrons facilitated static rearing posture.
HABITS Medium- to high-level browsers. Too slow to flee attackers, so spun around to keep spiny tail toward enemies.
NOTES Late Cretaceous *Dravidosaurus blanfordi* is probably a plesiosaur rather than a stegosaur.



Stegosaurus
shaded skull



Stegosaurus
muscle study

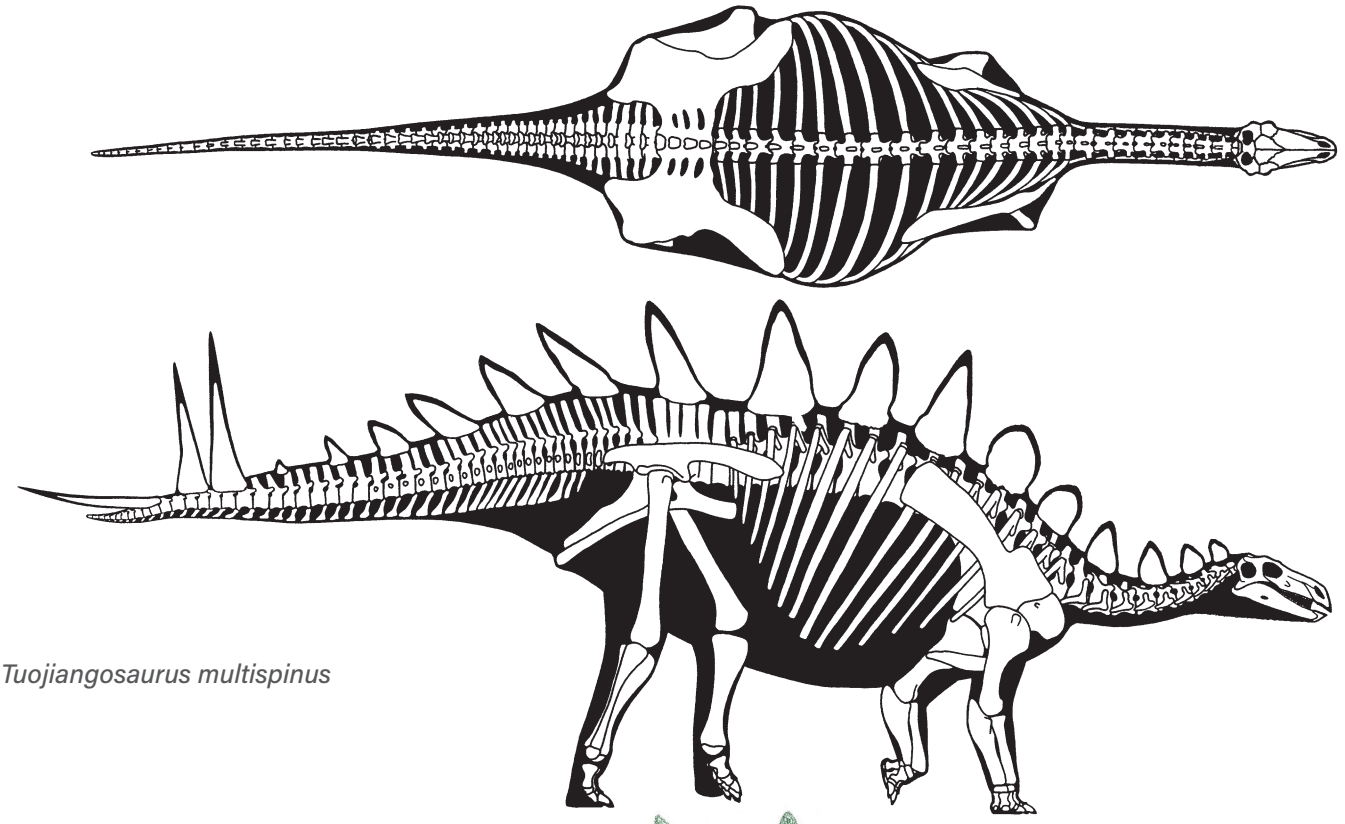
Jiangjunosaurus junggarensis
— 6 m (20 ft) TL, 2.5 tonnes
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.

Lexovisaurus durobrivensis
— 6 m (20 ft) TL, 2.5 tonnes
FOSSIL REMAINS A few partial skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip broad. Limbs fairly short. Long spine on shoulder. Main armor intermediate between plates and spines in shape.
AGE Middle Jurassic, Callovian.
DISTRIBUTION AND FORMATION/S Eastern England; lower Oxford Clay.

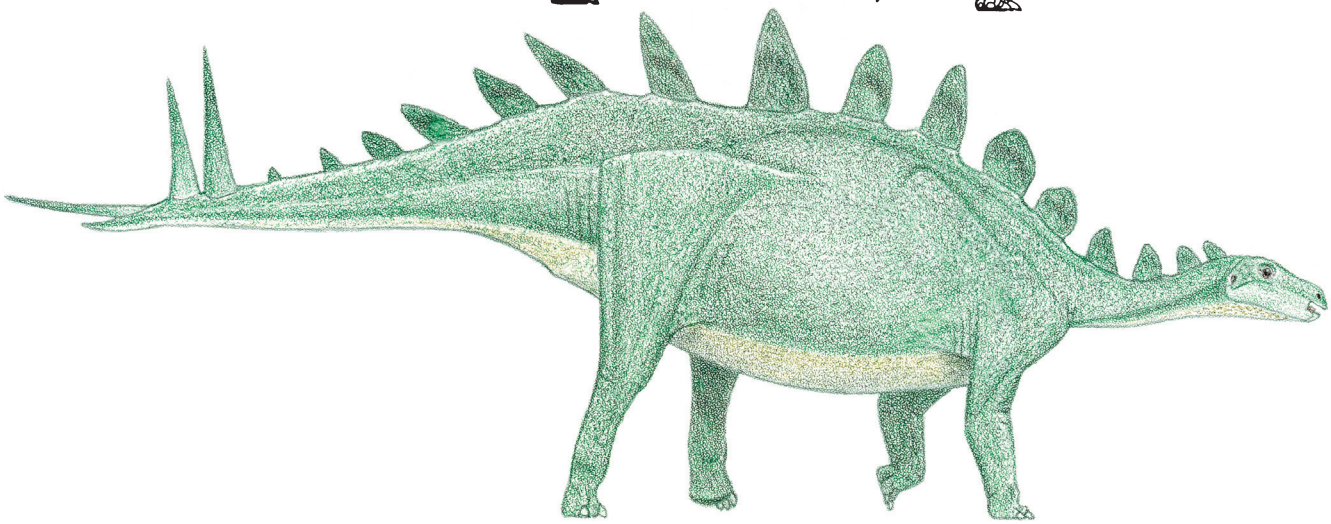
Tuojiangosaurus multispinus
— 6.5 m (22 ft) TL, 3.1 tonnes
FOSSIL REMAINS Minority of skulls and majority of a few skeletons, juvenile to adult.

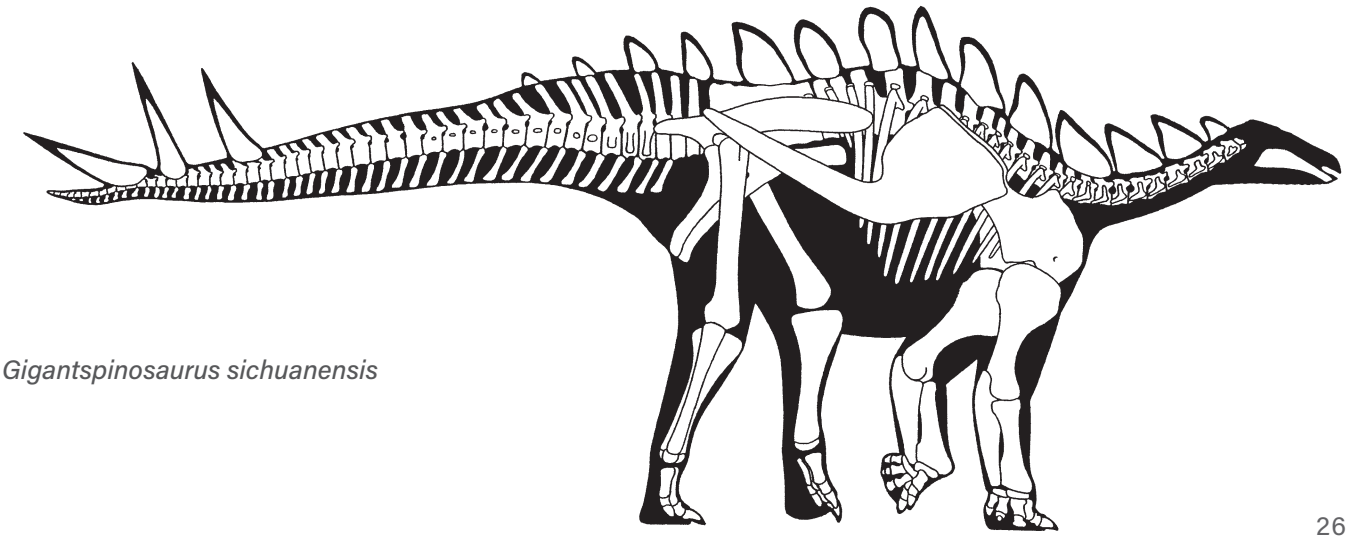
medium-sized plates, middle and tail plates taller, sharp tipped. Three pairs of terminal tail spines with first two erect, last pair directed backward, forming pincushion array.
AGE Late Jurassic, probably Oxfordian.
DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.
HABITAT/S Heavily forested.
NOTES *Chungkingosaurus jiangbeiensis* and *Chialingosaurus kuani* may be juveniles of at least this genus.

Gigantspinosaurus sichuanensis
— 4.2 m (14 ft) TL, 760 kg (1,700 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton, skin traces.
ANATOMICAL CHARACTERISTICS Belly and hip very broad. Limbs short. Top armor includes small plates and



Tuojiangosaurus multispinus





Gigantspinosaurus sichuanensis

spikes, arrangement of those of tail uncertain, exact orientation of enormous shoulder spike uncertain.
AGE Late Jurassic, probably Oxfordian.
DISTRIBUTION AND FORMATION/S Central China; lower Shangshaximiao.
HABITAT/S Heavily forested.

Kentrosaurus aethiopicus

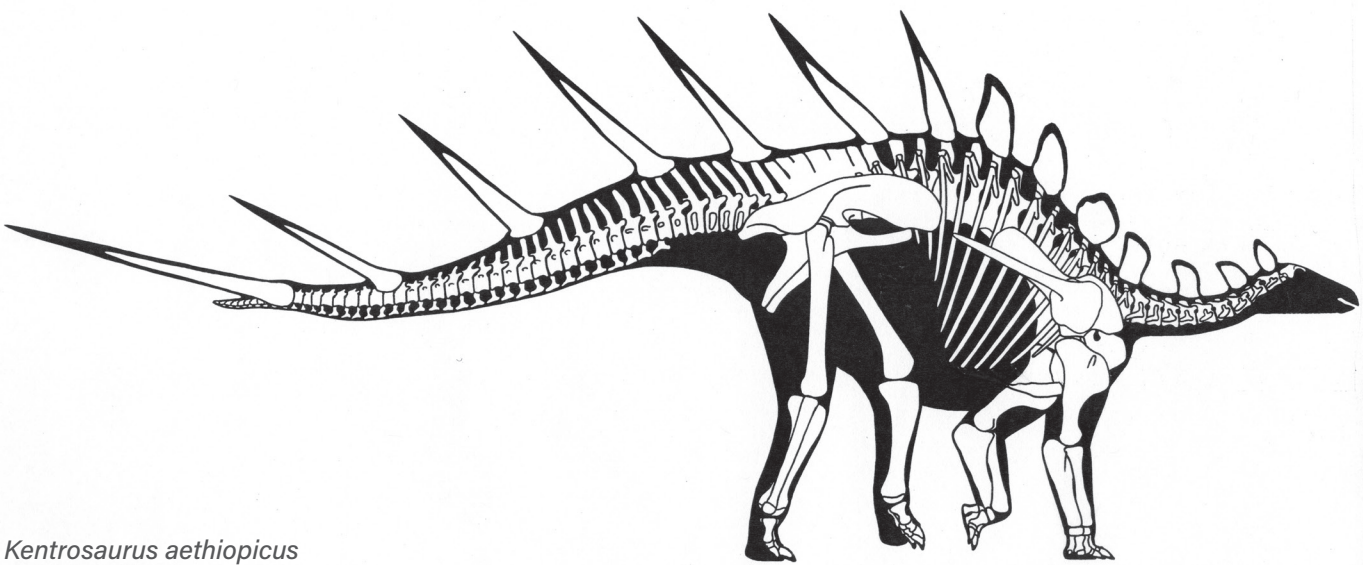
— 4 m (13 ft) TL, 740 kg (1,600 lb)
FOSSIL REMAINS A large number of partial skeletons and bones, juvenile to adult.
ANATOMICAL CHARACTERISTICS Belly and hip broad. Limbs fairly short. Front armor medium-sized plates, transitioning into long tail spines, long spine on shoulder.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Tanzania; middle Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Remains from much earlier lower Tendaguru and much later upper Tendaguru are not same taxon. Shoulder spine was long thought to be on hip.

Adratiklit boulahfa

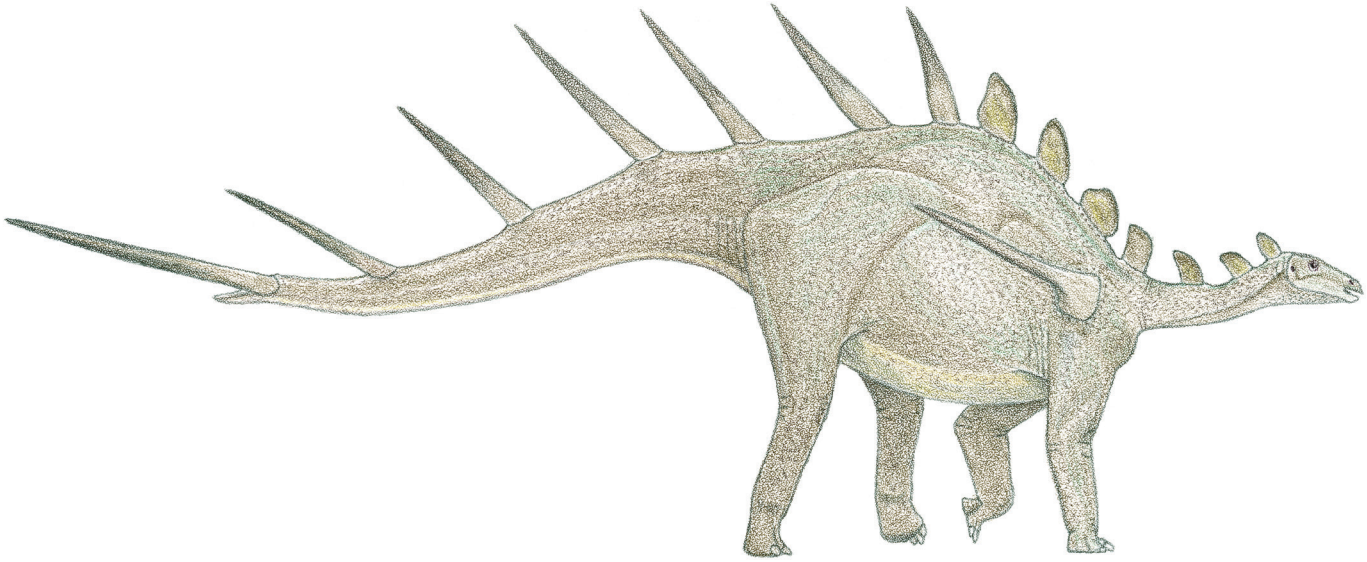
— 7 m (23 ft) TL, 4 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Middle Jurassic, Bathonian.
DISTRIBUTION AND FORMATION/S Morocco; El Mers II?

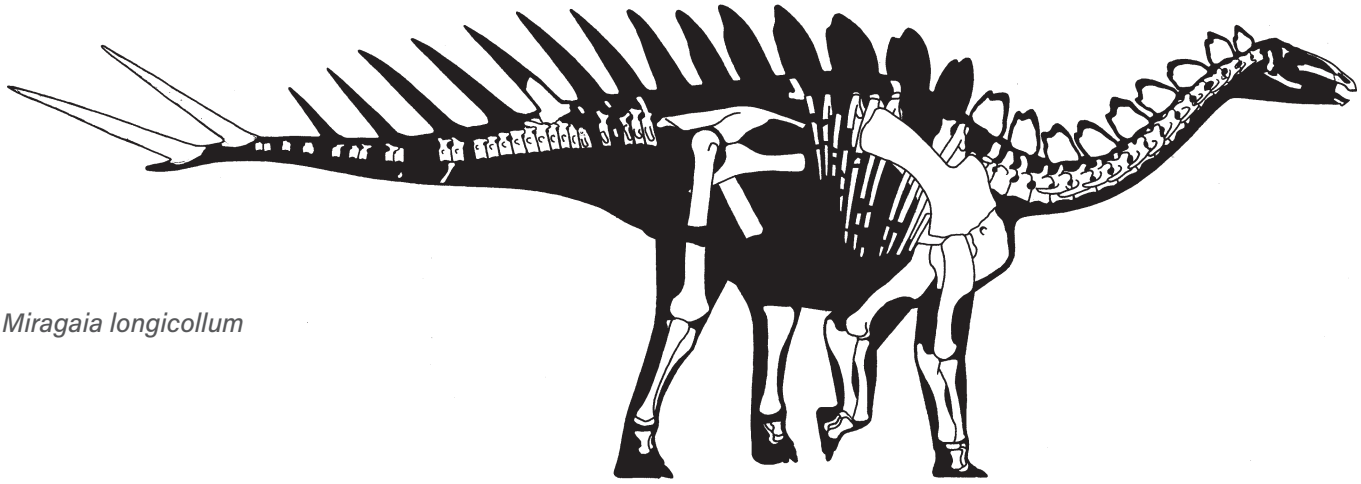
Dacentrurus armatus

— 8 m (25 ft) TL, 6 tonnes
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip very broad. Limbs fairly short.
AGE Late Jurassic, Kimmeridgian, possibly Tithonian.



Kentrosaurus aethiopicus





Miragaia longicollum

DISTRIBUTION AND FORMATION/S England, possibly other parts of western Europe; Kimmeridge Clay, possibly a number of other formations.
NOTES Whether all the fossils assigned to this species actually belong is uncertain.

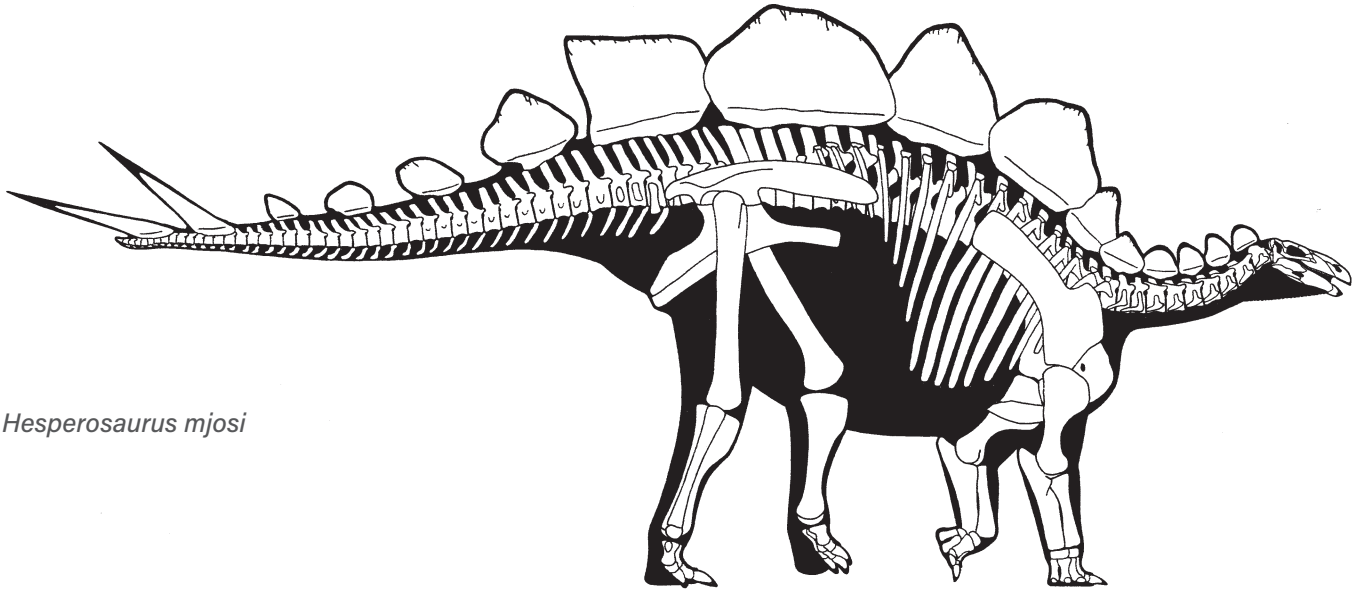
Miragaia (or *Alcovasaurus*) *longispinus*
— 6 m (20 ft) TL, 1.5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Terminal tail spines extremely long and slender.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Placement in *Miragaia* not certain.

Miragaia longicollum
— 6.5 m (20 ft) TL, 1.8 tonnes
FOSSIL REMAINS Two partial skulls and skeletons, other remains.
ANATOMICAL CHARACTERISTICS Head long and low. Neck as long as trunk. Main armor includes small paired plates each with small aft auxiliary projection atop neck; tail spines, at least some, large and long.
AGE Late Jurassic, early or middle Tithonian.
DISTRIBUTION AND FORMATION/S Portugal; middle Lourinhã.
HABITAT/S Large, seasonally dry island with open woodlands.
HABITS Well adapted for high browsing; long neck may also have been used for display.

Wuerhosaurus homheni
— 7 m (23 ft) TL, 4 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Belly and hip very broad. Limbs fairly short. Plates long and low.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Lianmuqin.
NOTES Not a species of *Stegosaurus*, as has been suggested.

Wuerhosaurus? *ordosensis*
— 5 m (16 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Neck probably elongated, trunk short. Belly and hip very broad.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Northern China; Ejinhoro.
NOTES Whether this is the same taxon as *W. homheni* or a different genus is uncertain.

Hesperosaurus mjosi
— 6.5 m (21 ft) TL, 3.5 tonnes
FOSSIL REMAINS Complete skull and some skeletons, adult and immature, skin traces.
ANATOMICAL CHARACTERISTICS Head shallow. Trunk short and deep, belly and hip narrow and slab sided. Leg long. Alternating armor plates large over trunk and tail, two pairs of spines form subhorizontal pincushion array.
AGE Late Jurassic, late Oxfordian.
DISTRIBUTION AND FORMATION/S Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.



Hesperosaurus mjosi

NOTES Although very similar in overall form to *Stegosaurus*, many differing details of skull anatomy require generic distinction. Gender differences may be reflected in differing plate size and sharpness of tips.

Stegosaurus stenops

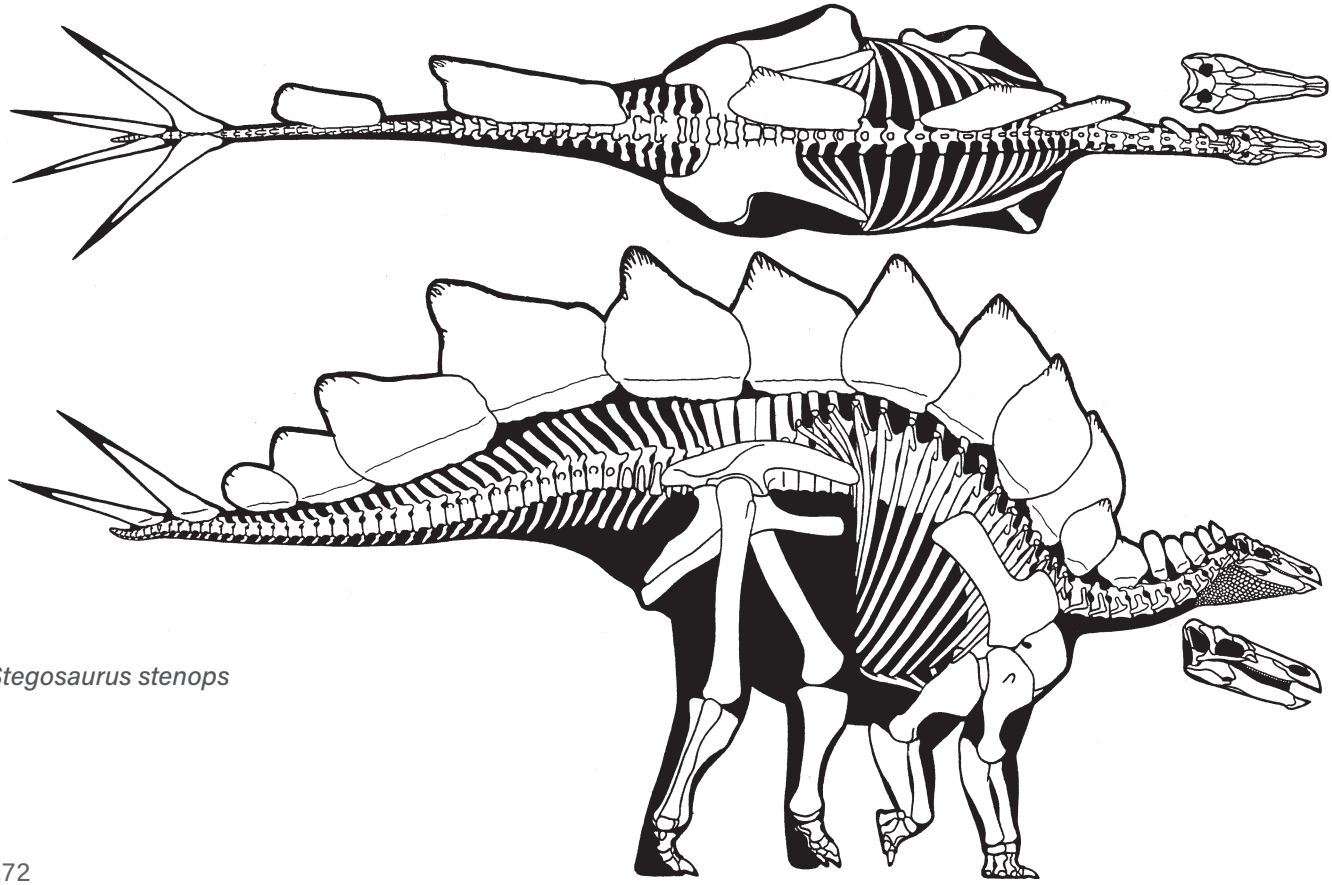
— 6.5 m (21 ft) TL, 3.5 tonnes

FOSSIL REMAINS Two complete skulls and several skeletons nearly complete to partial, many more partial remains and plates, completely known.

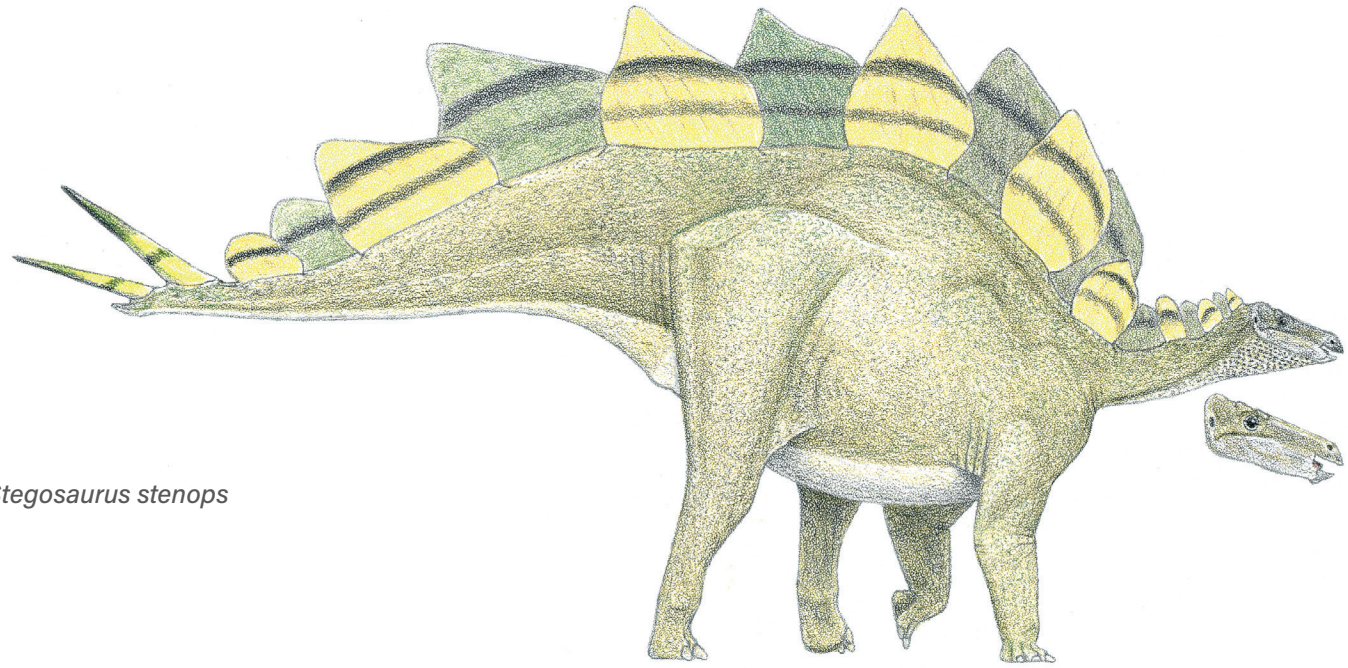
ANATOMICAL CHARACTERISTICS Head shallow. Trunk short and deep, belly and hip narrow and slab sided. Leg long. Seventeen alternating, very large armor plates over trunk and tail, tips somewhat rounded, two pairs of spines form subhorizontal pincushion array at end of S-curved tail tip, spines may have been massive when fully mature.

AGE Late Jurassic, early and/or early middle Kimmeridgian.

DISTRIBUTION AND FORMATION/S Colorado; middle Morrison.



Stegosaurus stenops



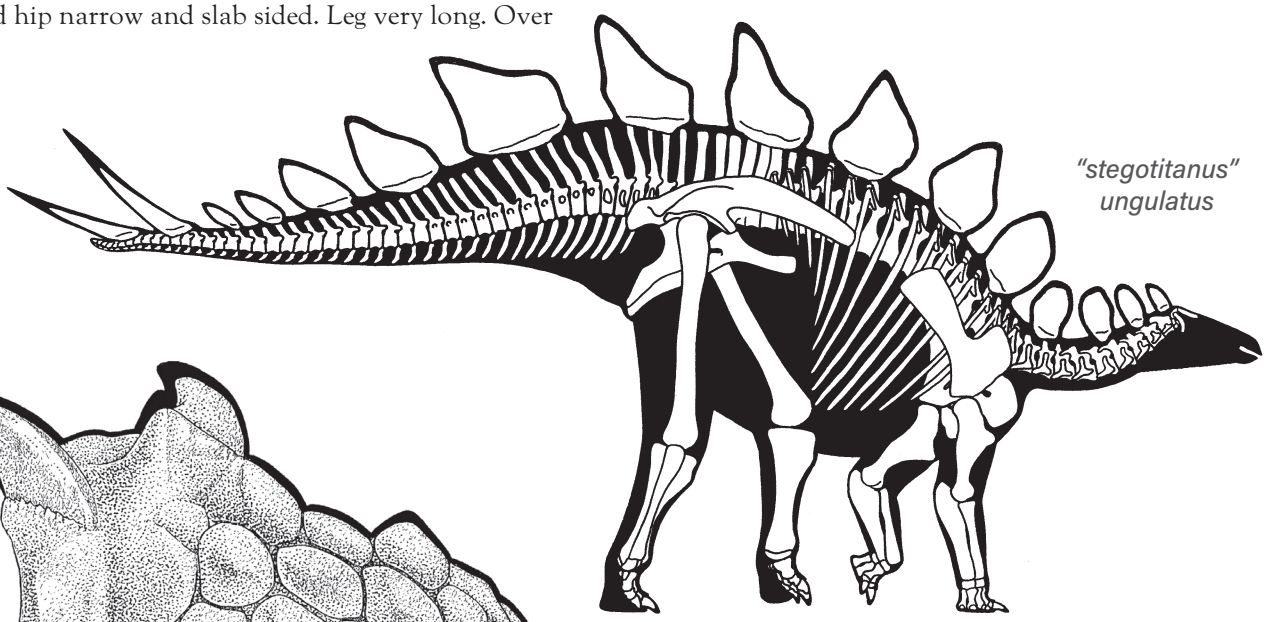
Stegosaurus stenops

Allosaurus fragilis and *Stegosaurus stenops*

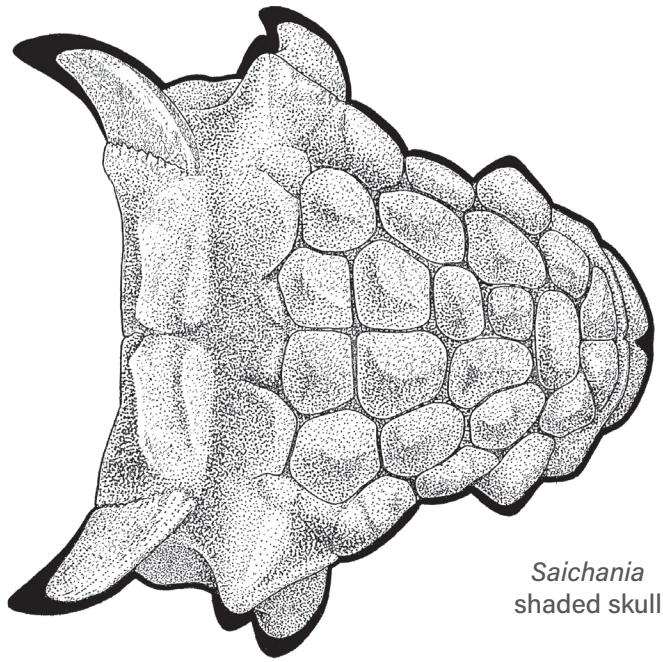
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Very well adapted for rearing, may have been able to walk slowly bipedally. Broken and healed spines and wound in *Allosaurus* tail show it used tail spine array as a weapon.
NOTES May have included large *S. sulcatus*, which has massive tail spines.

"stegotitanus" ungulatus

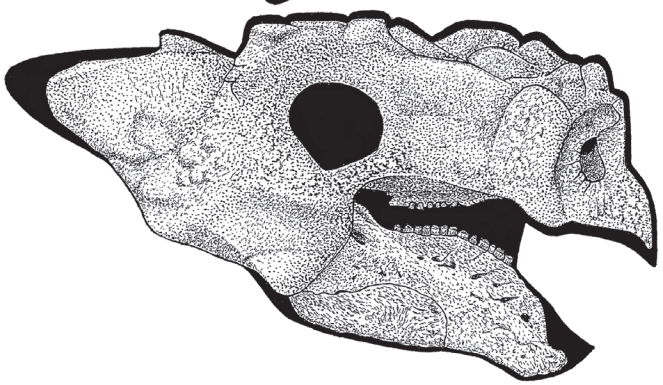
— 7 m (23 ft) TL, 4.2 tonnes
FOSSIL REMAINS Two partial skeletons, many partial remains and plates.
ANATOMICAL CHARACTERISTICS Trunk short and deep, belly and hip narrow and slab sided. Leg very long. Over two dozen fairly large, paired armor plates over trunk and tail, tips pinched and sharp.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; upper Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
HABITS Very well adapted for rearing, may have been able to walk slowly bipedally.
NOTES Was in *Stegosaurus*. Earlier species of genus may have been present in middle Morrison. Possibility of four pairs of tail spines has not been confirmed.



"stegotitanus" ungulatus



Saichania shaded skull

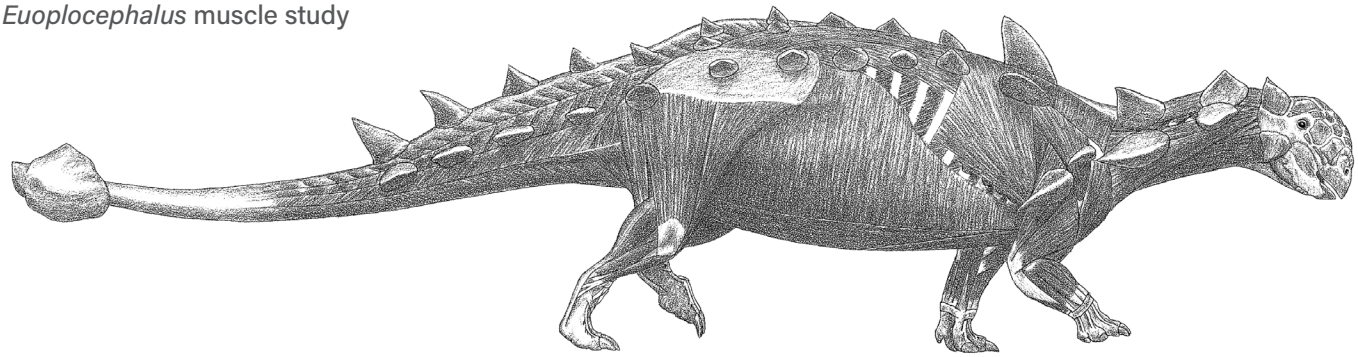


— ANKYLOSAURS

MEDIUM-SIZED TO VERY LARGE EURYPOD THYREOPHORANS FROM THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads massively constructed, broad, nasal passages large, usually no teeth under upper beaks, main tooth rows short, teeth smaller. Voice boxes complex, necks short and straight. Aft ribs fused to vertebrae, trunks long and shallow, bellies and hips very to extremely broad. Shoulders and hips usually about same height, or shoulders a little lower. Tail bases sweep down from hips, tails held low above ground, moderately long. Quadrupedal, shoulders as high as hips, arms and legs short but flexed, so able to run slowly. Four or three toes. Always extensive armor variable, always includes longitudinal and transverse rows of large scutes covering most of top of necks, trunks, and tails. Unarmored skin standard for dinosaurs.

Euoplocephalus muscle study



HABITAT/S Very variable, from deserts to well-watered forests.
HABITS Usually low-level browsers and grazers. Probably hunkered down on belly and used armor to avoid being wounded while using the great breadth of the trunk to prevent being overturned. Good diggers with stout, broad-handed arms, juveniles and adults of smaller species probably burrowed, large adults may have excavated depressions for improved protection against predators and cold or hot weather.
NOTES The most heavily armored dinosaurs, and the dinosaurs most similar to turtles and glyptodonts, although not as extensively armored. Skull armor sometimes coalesced, obscuring details of skull. Middle Jurassic fragmentary *Spicomellus afer* affirms presence of group in Africa.

— NODOSAURIDS

MEDIUM-SIZED TO LARGE ANKYLOSAURS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, BOTH HEMISPHERES.

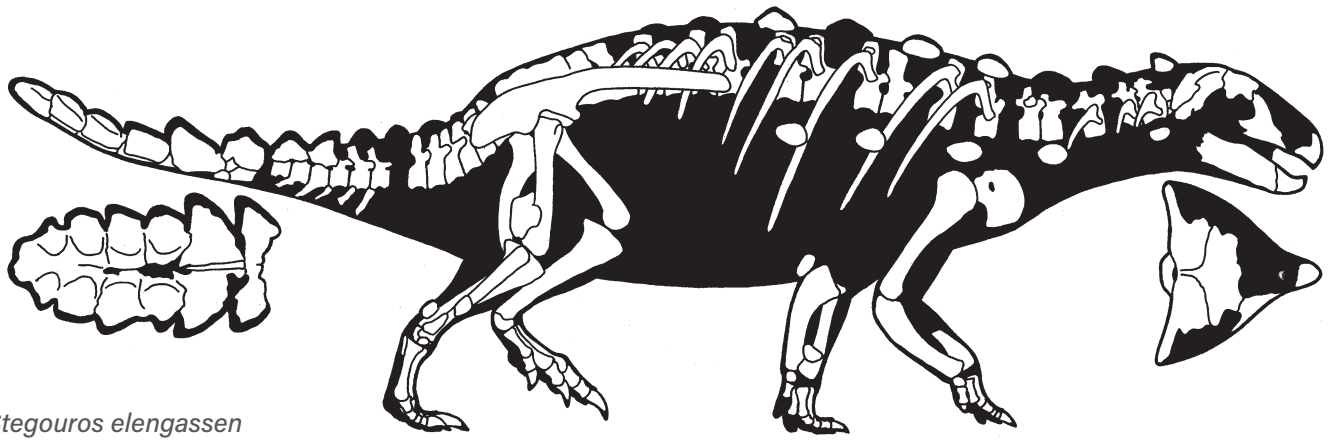
ANATOMICAL CHARACTERISTICS Some have teeth under upper beak. Some have an armor pelvic shield. Tail club absent.
HABITS Defense included hunkering down on belly and using armor plates and spikes to avoid being wounded while using the great breadth of the trunk to prevent being overturned, and dashing into heavy brush when possible.
NOTES Probably divisible into multiple groups that have yet to be reliably determined. Latest examples may have matched last ankylosaurids in size.

Antarctopelta oliveroi

— 6 m (20 ft) TL, 400 kg (900 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Western Antarctica; Santa Marta.
HABITAT/S Polar forests with warm, daylight-dominated summers and cold, dark winters.
NOTES That this is the only ankylosaur yet named from Antarctica reflects difficult conditions and the lack of more extensive exposed deposits.

Stegouros elengassen

— 1.55 m (5 ft) TL, 80 kg (180 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head large, very broad at back, snout narrow in top view. Legs relatively short.

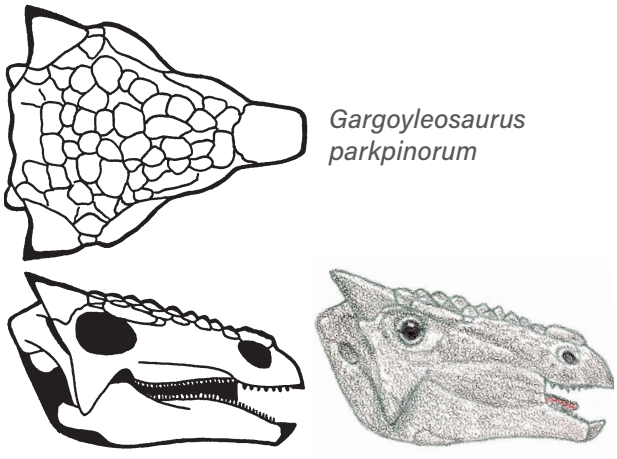


Stegouros elengassen

Tail short, base strongly downturned, latter portion lined by series of large, sideways-projecting triangular plates, otherwise lightly armored.
AGE Late Cretaceous, late Campanian and/or late Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Chile; lower Dorotea.

Mymoorapelta maysi
— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Minority of skull and several skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic.
DISTRIBUTION AND FORMATION/S Colorado; Morrison, level uncertain.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Dracopelta zbyszewskii
— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS No shoulder spines.
AGE Late Jurassic, late Tithonian.
DISTRIBUTION AND FORMATION/S Portugal; upper Lourinhã.
HABITAT/S Large, seasonally dry island with open woodlands.



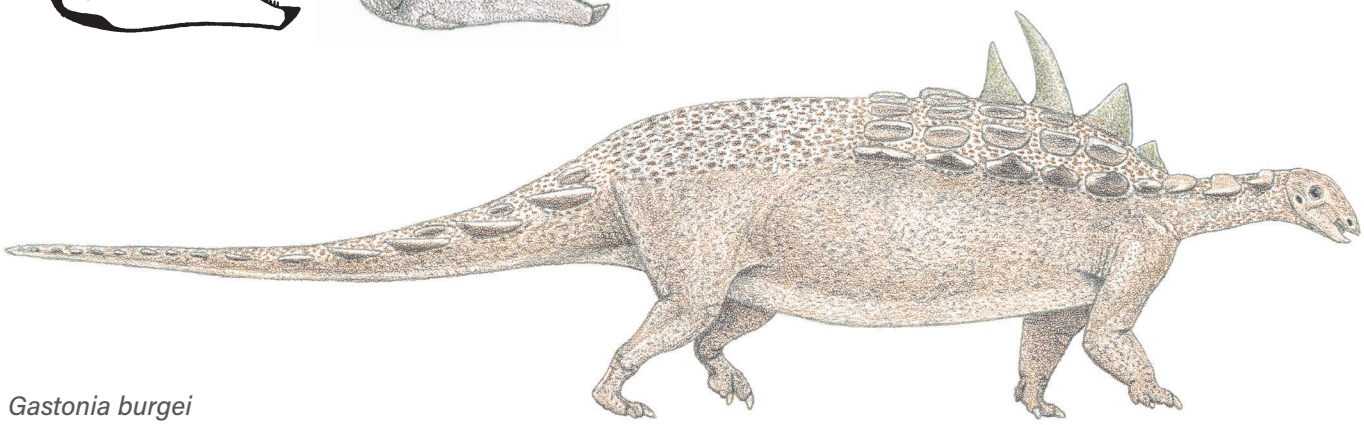
Gargoyleosaurus parkpinorum

Hylaeosaurus armatus
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Long, backward-directed shoulder spines.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; Grinstead Clay.
NOTES Another fossil has been removed from taxon, leaving only the original fossil.

Gargoyleosaurus parkpinorum
— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Complete skull, minority of skeleton.
ANATOMICAL CHARACTERISTICS Head heavily armored, seven teeth under upper beak.
AGE Late Jurassic, late middle and/or late? Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; probably upper Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Hoplitosaurus marshi
— 4.5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Skeletons.
ANATOMICAL CHARACTERISTICS Armor includes spines, arrangement uncertain.
AGE Early Cretaceous, probably Barremian.
DISTRIBUTION AND FORMATION/S South Dakota; Lakota.

Gastonia burgei
— 5 m (17 ft) TL, 2.2 tonnes
FOSSIL REMAINS A few skulls and skeletons from nearly complete to partial.
ANATOMICAL CHARACTERISTICS Head very small, heavily armored, no teeth under upper beak. Arm and leg very short. Belly extremely broad. Rows of large vertical and horizontal shoulder spines, no lateral spines at hip, modest spines on side of tail.
AGE Early Cretaceous, late Valanginian.



Gastonia burgei

DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Gastonia? lorriemcwhinneyae
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skull and partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Utah; middle Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
NOTES May not be same genus as much earlier *G. burgei*.

Peloroplites cedrimontanus
— 6 m (20 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skull and almost complete skeleton known from partial fossils.
ANATOMICAL CHARACTERISTICS Head shallow.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Utah; upper Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Polacanthus foxii
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Belly very broad. Armor includes spines, arrangement uncertain.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Southern England; upper Wessex.
NOTES Some fossils have been removed from taxon, leaving only the original fossil.

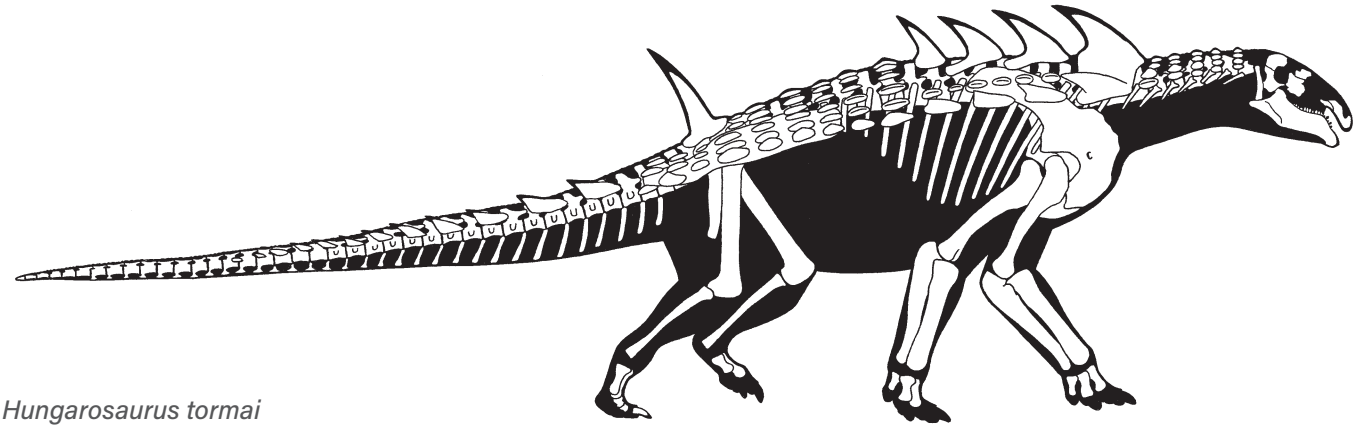
Zhejiangosaurus lishuiensis
— 4.5 m (15 ft) TL, 1.4 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Head shallow.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Eastern China; Chaochuan.

Hungarosaurus tormai
— 4.8 m (16 ft) TL, 1.2 tonne
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Arm long, so shoulder higher than hip. Two rows of four large spines over and on side of shoulder, pair of modest pelvic spines set on conjoined plate.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Hungary; Csehbánya.
HABITS High browser rather than ground grazer.
NOTES Only ankylosaur known to have high shoulder.

Struthiosaurus austriacus
— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Minority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip very broad.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Austria, Southern France; Gosau, unnamed formation.
HABITAT/S Forested island.
NOTES *S. languedocensis* may be the adult of this species. Small size may be dwarfism due to island habitat.

Struthiosaurus transylvanicus
— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Partial skull and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Romania; Sânpetru.
HABITAT/S Forested island.
NOTES May be the descendant of *S. austriacus*.

Unnamed genus and species
— 7+ m (25 ft) TL, 6+ tonnes
FOSSIL REMAINS Minority of skeleton.



Hungarosaurus tormai

ANATOMICAL CHARACTERISTICS Pelvic shield present.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Wyoming, lower Lance.
HABITAT/S Well-watered coastal woodlands.
NOTES Last known continental nodosaur with pelvic shield. Probably largest known nodosaur, approached and may have rivaled *Ankylosaurus* in size.

Animantarx ramaljonesi

— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Utah; uppermost Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Niobrarasaurus coleii

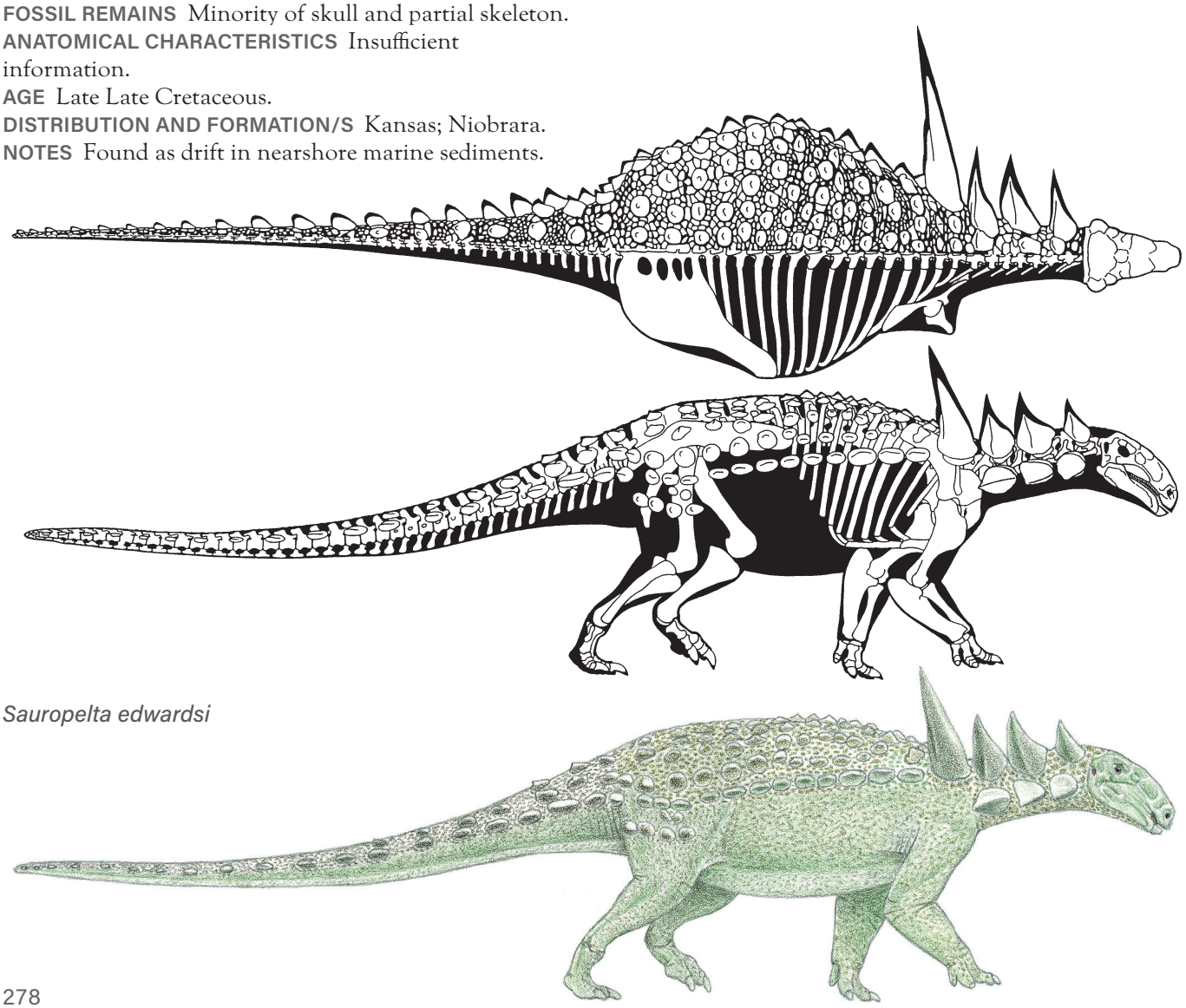
— 6.5 m (21 ft) TL, 3.5 tonnes
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Late Cretaceous.
DISTRIBUTION AND FORMATION/S Kansas; Niobrara.
NOTES Found as drift in nearshore marine sediments.

Nodosaurus textilis

— 6 m (20 ft) TL, 3 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Wyoming; lower Frontier.
NOTES Found as drift in nearshore marine sediments.

Sauropelta edwardsi

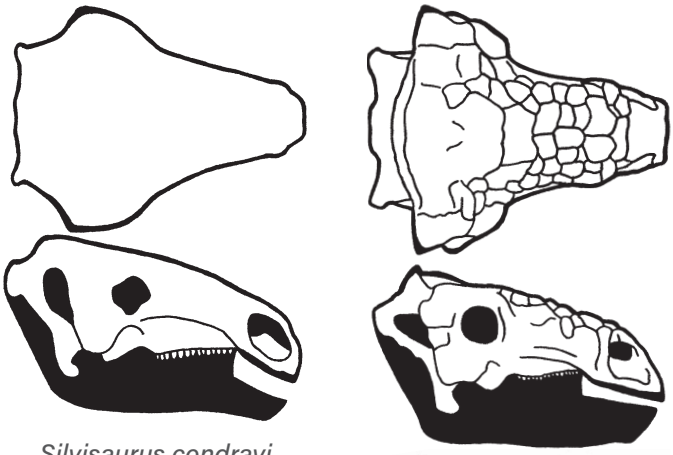
— 6 m (20 ft) TL, 2.3 tonnes
FOSSIL REMAINS Several partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip very broad. Tail long. Two rows of three large spines on side of neck, very large and slightly split spine on shoulder.
AGE Early Cretaceous, late Aptian to lower Albian.
DISTRIBUTION AND FORMATION/S Wyoming; Cloverly.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
NOTES *Tatankacephalus cooneyorum* is probably the juvenile of this taxon.



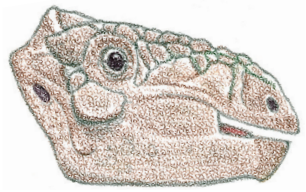
Sauropelta edwardsi

Stegopelta landerensis
— 4 m (12 ft) TL, 1 tonne
FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Wyoming; Frontier.
NOTES Found as drift in nearshore marine sediments.

Silvisaurus condrayi
— 4 m (12 ft) TL, 1 tonne
FOSSIL REMAINS Skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS No teeth under upper beak.



Silvisaurus condrayi



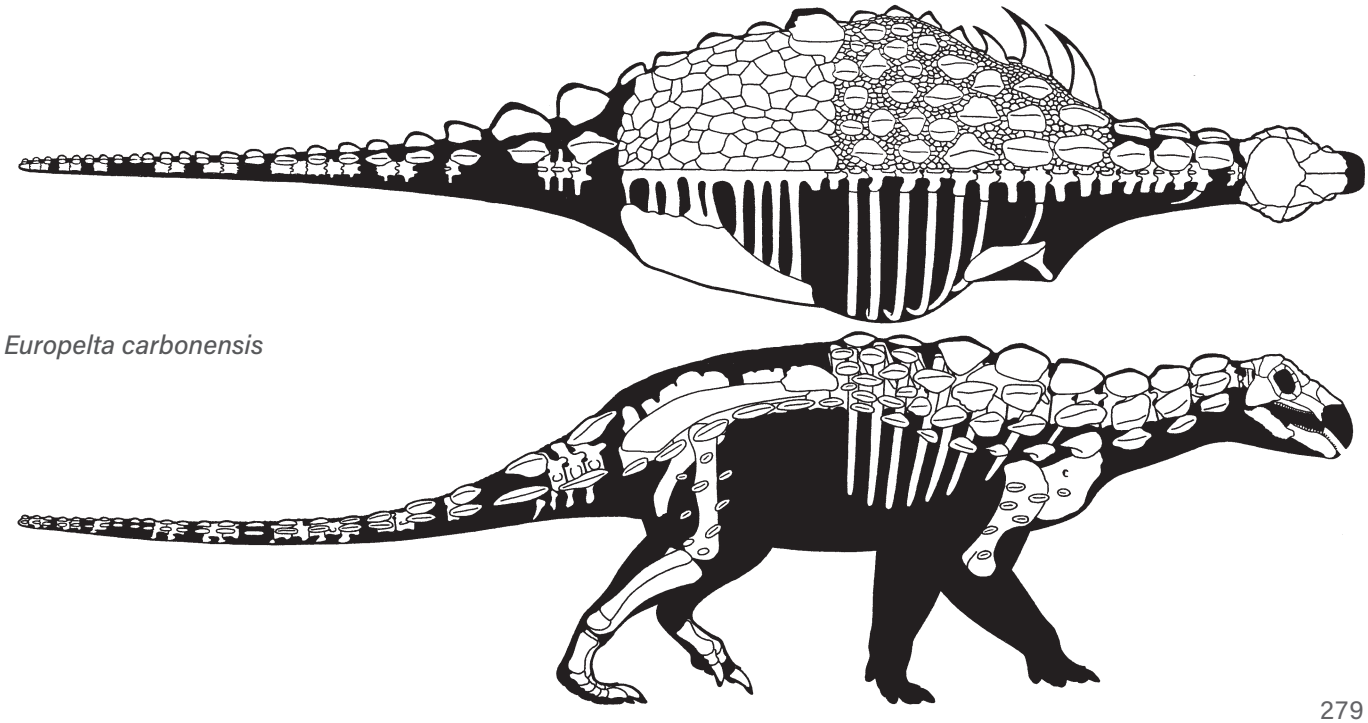
Pawpawsaurus campbelli

AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Kansas; Dakota.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.
NOTES One of the few dinosaurs found on the eastern shore of the interior seaway.

Propanoplosaurus marylandicus
— Adult size uncertain
FOSSIL REMAINS Complete skull and half of skeleton, poorly preserved.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Aptian.
DISTRIBUTION AND FORMATION/S Maryland; Patuxent.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.

Pawpawsaurus campbelli
— Adult size uncertain
FOSSIL REMAINS Skull and minority of a skeleton, juveniles.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Texas; Paw Paw.
NOTES Probably includes *Texasetes pleurohalio*. Found as drift in nearshore marine sediments.

Europelta carbonensis
— 5 m (16 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip moderately broad. Limbs fairly long. Two prominent horizontal spikes on shoulder.

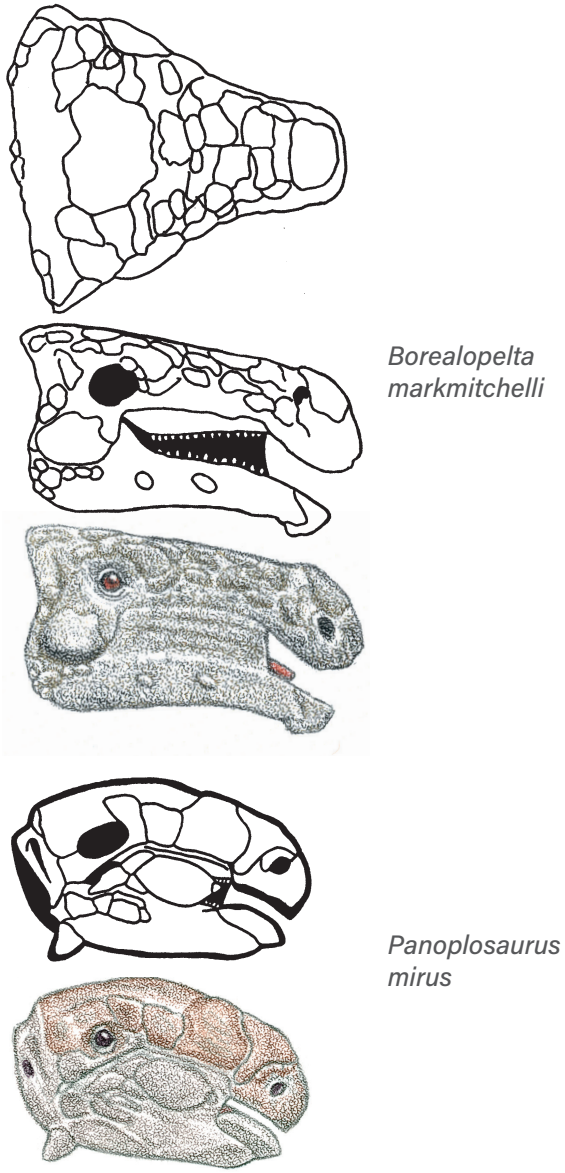


Europelta carbonensis

AGE Early Cretaceous, early Albian.
DISTRIBUTION AND FORMATION/S Spain; Escucha.
HABITAT/S Coastal.

Borealopelta markmitchelli

— 5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Complete skull and partial skeleton with keratin armor sheaths and skin, stomach contents.
ANATOMICAL CHARACTERISTICS No teeth under upper beak. Neck and shoulder spines modest in size. Upper body darker than underside.
AGE Early Cretaceous, earliest Albian.
DISTRIBUTION AND FORMATION/S Alberta; lower Clearwater.
HABITAT/S Found as drift in nearshore marine sediments.
HABITS Stomach contents show last meals were ground ferns.
NOTES Armor coverage of forward half and absence of last half of extraordinary fossil's skeleton preclude skeletal restoration. Skull illustration is not a profile image because skull is preserved with its keratin covering.



Borealopelta markmitchelli

Panoplosaurus mirus

Panoplosaurus mirus

— 5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Complete skull and majority of skeletons.
ANATOMICAL CHARACTERISTICS Armor plate covered cheeks, large spines absent.
AGE Late Cretaceous, early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; at least middle Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Edmontonia rugosidens

— 6 m (19 ft) TL, 3.7 tonnes
FOSSIL REMAINS Several complete skulls and majority of skeletons.
ANATOMICAL CHARACTERISTICS Belly and hip extremely broad. Armor plate covered cheeks, large, forward-directed spikes on flank of neck and shoulder, one spine partly split, no spines on main trunk or hips.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana, Alberta?; upper Two Medicine, lower and middle Dinosaur Park?, upper Judith River?
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and drier upland woodlands.
HABITS *Edmontonia* may have charged at opponents within species and tyrannosaurids with shoulder spikes.
NOTES May be direct ancestor of *E. longiceps*.

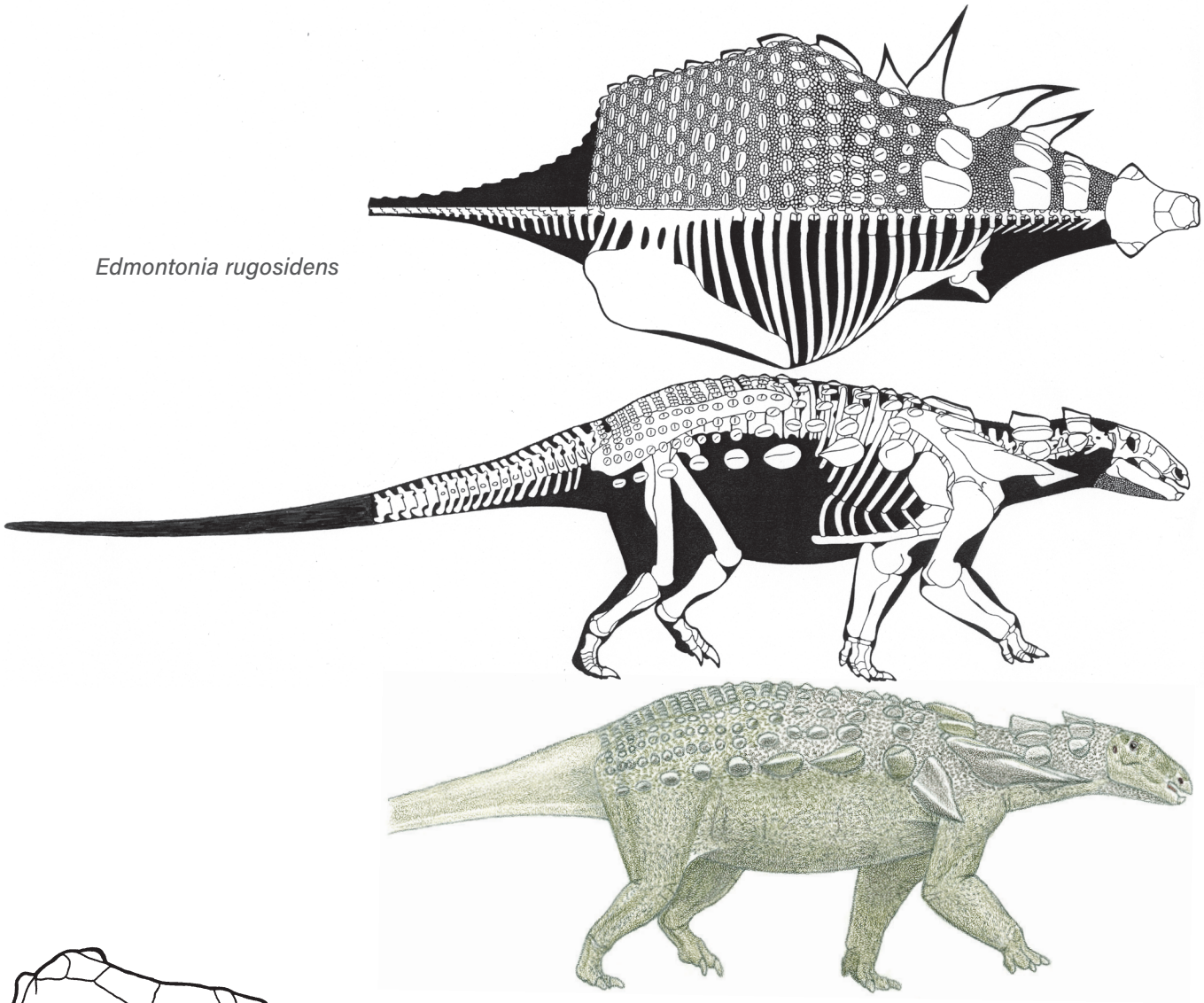
Edmontonia longiceps

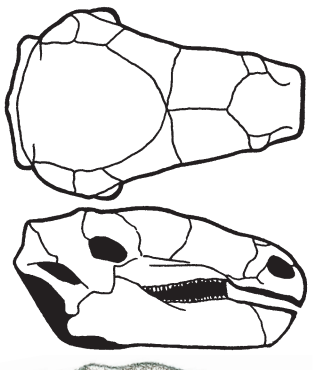
— 6 m (19 ft) TL, 3.5 tonnes
FOSSIL REMAINS Several complete skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS Shoulder spikes modest sized, directed sideways.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta, Montana; lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be an ancestor of *E. schlessmani*.

Edmontonia (= *Denversaurus*) *schlessmani*

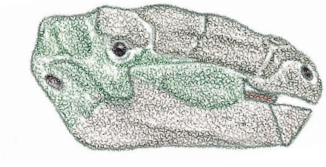
— 6 m (19 ft) TL, 3.5 tonnes
FOSSIL REMAINS Complete skull, minority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S South Dakota, Montana; Hell Creek.
HABITAT/S Forested floodplain with coastal swamps and marshes, cool winters.

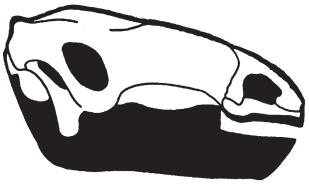
Edmontonia rugosidens





Edmontonia longiceps





Edmontonia (=*Denversaurus*) *schlessmani*

Zhongyuansaurus luoyangensis

— 5 m (15 ft) TL, 2 tonnes

FOSSIL REMAINS Majority of crushed skull, minority of skeleton.

ANATOMICAL CHARACTERISTICS Head probably shallow, heavily armored, no teeth under upper beak.

AGE Late Cretaceous.

DISTRIBUTION AND FORMATION/S Eastern China; Haoling.

Minmi paravertebra

— 3 m (9 ft) TL, 350 kg (700 lb)

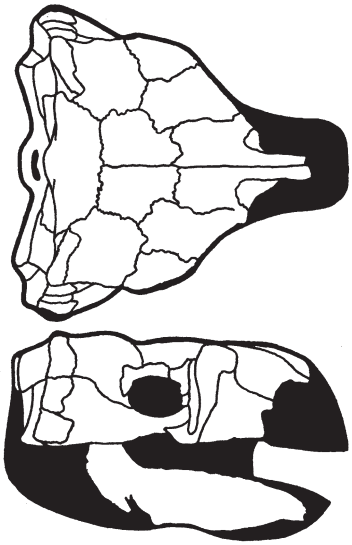
FOSSIL REMAINS Minority of skeleton.

ANATOMICAL CHARACTERISTICS Insufficient information.

AGE Early Cretaceous, Aptian.

DISTRIBUTION AND FORMATION/S Northeastern Australia; Bungil.

HABITAT/S Lagoon bordered by polar forests with warm, daylight-dominated summers and cold, dark winters.



Kunburrasaurus leversi

Kunbarrasaurus leversi

— 3 m (9 ft) TL, 350 kg (700 lb)
FOSSIL REMAINS A few skulls and skeletons from majority to partial.
ANATOMICAL CHARACTERISTICS Head subrectangular because snout is as deep as back of head, which is flat topped, lightly armored, and broad.
AGE Early Cretaceous, late Albian and/or perhaps early Cenomanian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; Allaru.
HABITAT/S Found as marine drift from polar forests with warm, daylight-dominated summers and cold, dark winters.
NOTES Skeleton not yet sufficiently described for restoration.

Gobisaurus domoculus

— 6 m (20 ft) TL, 3.5 tonnes
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Head heavily armored.
AGE Late Cretaceous, Turonian.
DISTRIBUTION AND FORMATION/S Northern China; Wulansuhai.

Shamosaurus scutatus

— 5 m (15 ft) TL, 2 tonnes
FOSSIL REMAINS Two skulls, partial skeleton.
ANATOMICAL CHARACTERISTICS Head shallow, heavily armored, no teeth under upper beak. Neck armor forming cervical half rings.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Mongolia; Huhteeg Svita.

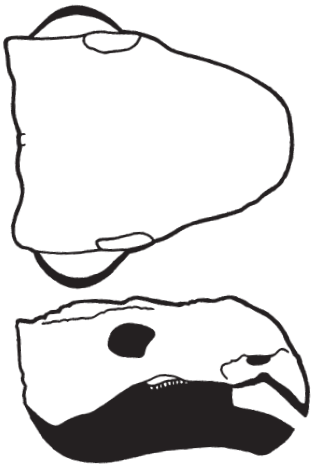
Cedarpelta bilbeyhallorum

— 7 m (23 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skull and almost complete skeleton known from very many partial fossils.
ANATOMICAL CHARACTERISTICS Head shallow, not heavily armored, teeth near front end of upper jaw.
AGE Early Cretaceous, late Albian.
DISTRIBUTION AND FORMATION/S Utah; upper Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Liaoningosaurus paradoxus

— Adult size uncertain
FOSSIL REMAINS Two almost complete distorted skulls and skeletons, juveniles.
ANATOMICAL CHARACTERISTICS Head heavily armored, juvenile teeth sharp. Belly and pelvis very broad. Juvenile claws sharp.
AGE Early Cretaceous, at least earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Sharp teeth and claws and stomach contents suggest at least juveniles were semiaquatic fishers.
NOTES Lack of mature fossil hinders full assessment of adult anatomy and habits.

Gobisaurus domoculus



Shamosaurus scutatus

Liaoningosaurus (= *Chuanqilong*) *chaoyangensis*

— Adult size uncertain
FOSSIL REMAINS Majority of almost complete distorted skull and skeleton, immature.
ANATOMICAL CHARACTERISTICS Teeth not sharp. Belly and pelvis very broad, tail rather short. Claws not sharp.
AGE Early Cretaceous, early or middle Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Jiufotang, level uncertain.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Lack of sharp teeth and claws indicates at least mature examples were conventional herbivores.
NOTES The one fossil is larger than those of *L. paradoxus* and more mature, but not fully adult. May be the more mature expression of *Liaoningosaurus*, younger geological age indicates is not the same species.

— ANKYLOSAURIDS

MEDIUM-SIZED TO VERY LARGE ANKYLOSAURS LIMITED TO THE CRETACEOUS OF NORTH AMERICA AND ASIA.

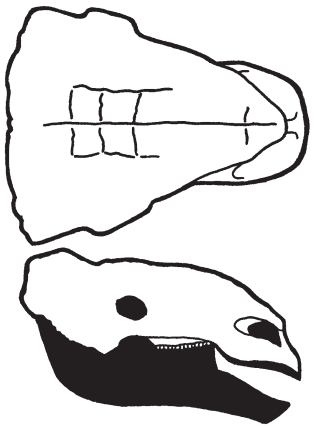
ANATOMICAL CHARACTERISTICS Beaks and overall heads broad, heads heavily armored with large triangular hornlets at the back corners, upper eyelids sometimes armored, no teeth under upper beaks. Bellies and hips very broad. Limbs short. Three toes. Large spines absent, two short spikes flanking necks, last half of tails stiffened by ossified rods and tipped with a club.
HABITS Low-level browsers and grazers. Defense included running while swinging clubbed tails to keep theropod from getting close to its victim, spinning around to keep tails toward attacker while using clubs to damage legs or flanks or to topple theropod, and dashing into heavy brush when possible. Tail clubs regularly used for display and combat within species.

Jinyunpelta sinensis

— Adult size uncertain
FOSSIL REMAINS Majority of badly damaged skull and partial skeletons, possibly immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Albian or early Cenomanian.
DISTRIBUTION AND FORMATION/S Eastern China; Liangtoutang.
NOTES Earliest ankylosaurine with preserved tail club.

Crichtonpelta benxiensis

— Adult size uncertain
FOSSIL REMAINS A few partial skulls and skeletons, possibly juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, late Albian?



Tsagantegia longicranialis

DISTRIBUTION AND FORMATION/S Northeastern China; Sunjiawan.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.

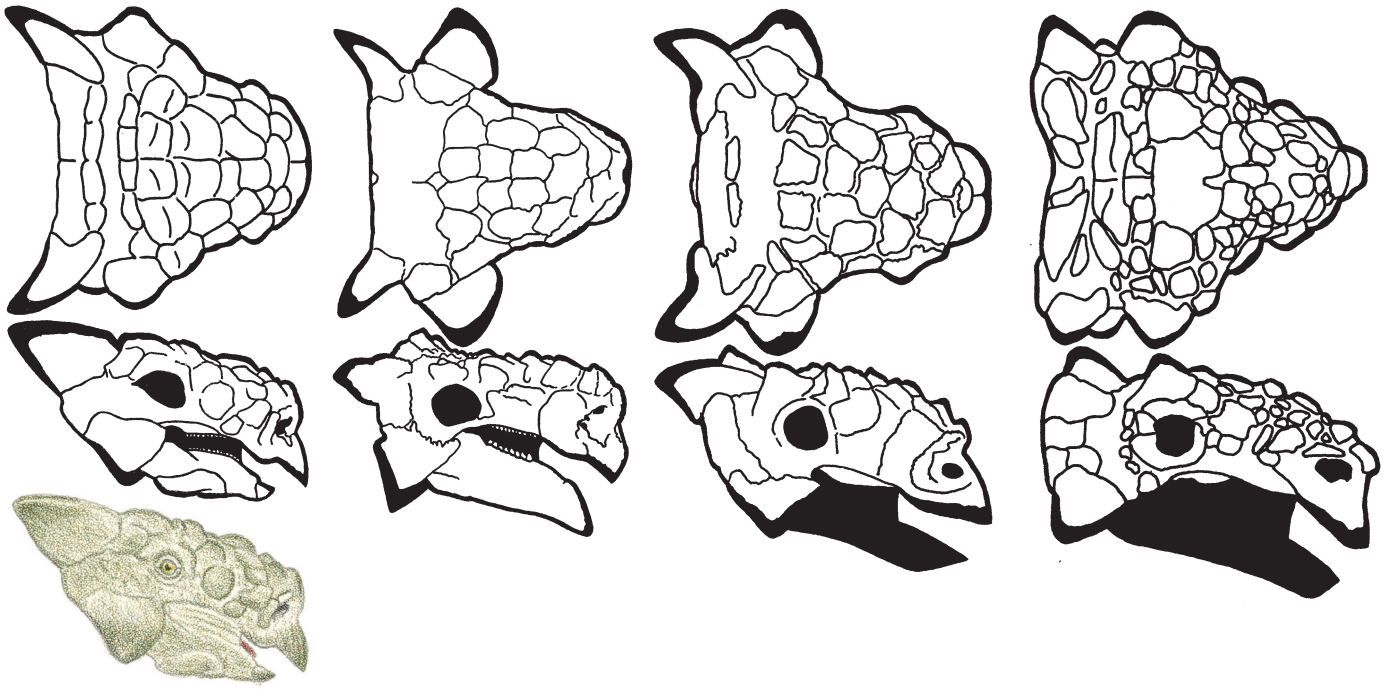
Tsagantegia longicranialis

— 3.5 m (12 ft) TL, 600 kg (1,300 lb)
FOSSIL REMAINS Skull.
ANATOMICAL CHARACTERISTICS Head shallow, upper beak rounded off.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Mongolia; Bayenshiree Svita.

Saichania chulsanensis

— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Complete and partial skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS Head subtriangular in side view, upper beak rounded off. Upper and lower temporal hornlets large and subequal in size. Tail club subcircular in top view.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia, northern China; upper? Barun Goyot, Huiquanpu.
NOTES May include partial *Zaraapelta nomadis* and fragmentary *Tarchia kielanae*, as well as Chinese *Tianzhenosaurus youngi* and *Shanxia tianzhenensis*, especially if the two formations are the same age; if not, the Mongolian and Chinese remains may at least be same genus. May be an ancestor of *Saichania teresae* or *S.tumanovae*.

Saichania chulsanensis | *Saichania* (or unnamed genus) *teresae*. | *Saichania* (or unnamed genus) *tumanovae* | *Talarurus plicatospineus*



Saichania (or unnamed genus) *teresae*

— 5.5 m (18 ft) TL, 2.5 tonnes

FOSSIL REMAINS Skull and partial skeleton.

ANATOMICAL CHARACTERISTICS Head subrectangular in side view because snout is deep, upper beak rounded, upper and lower temporal hornlets large and subequal in size.

AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.

DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.

HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

NOTES Usual placement in earlier, fragmentary *Tarchia* problematic.

Saichania (or unnamed genus) *tumanovae*

— 6 m (19 ft) TL, 3 tonnes

FOSSIL REMAINS Skull and partial skeleton.

ANATOMICAL CHARACTERISTICS Head subtriangular in side view, upper beak rounded, upper and lower temporal hornlets modest and subequal in size. Tail club large, subcircular in top view.

AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.

DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.

HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

NOTES Usual placement in earlier, fragmentary *Tarchia* problematic. May be a gender of *T. teresae*.

Talarurus plicatospineus

— 4.5 m (15 ft) TL, 1.5 tonnes

FOSSIL REMAINS Four complete to partial skulls, majority of skeleton.

ANATOMICAL CHARACTERISTICS Upper beak broad and squared off, upper and lower temporal hornlets subequal and modest in size.

AGE Early Late Cretaceous.

DISTRIBUTION AND FORMATION/S Mongolia; Bayenshiree Svita, level uncertain.

HABITAT/S Semiarid woodlands.

HABITS Grazed ground cover.

Pinacosaurus grangeri

— 5 m (17 ft) TL, 2 tonnes

FOSSIL REMAINS Numerous complete and partial skulls and skeletons from juvenile to adult, completely known.

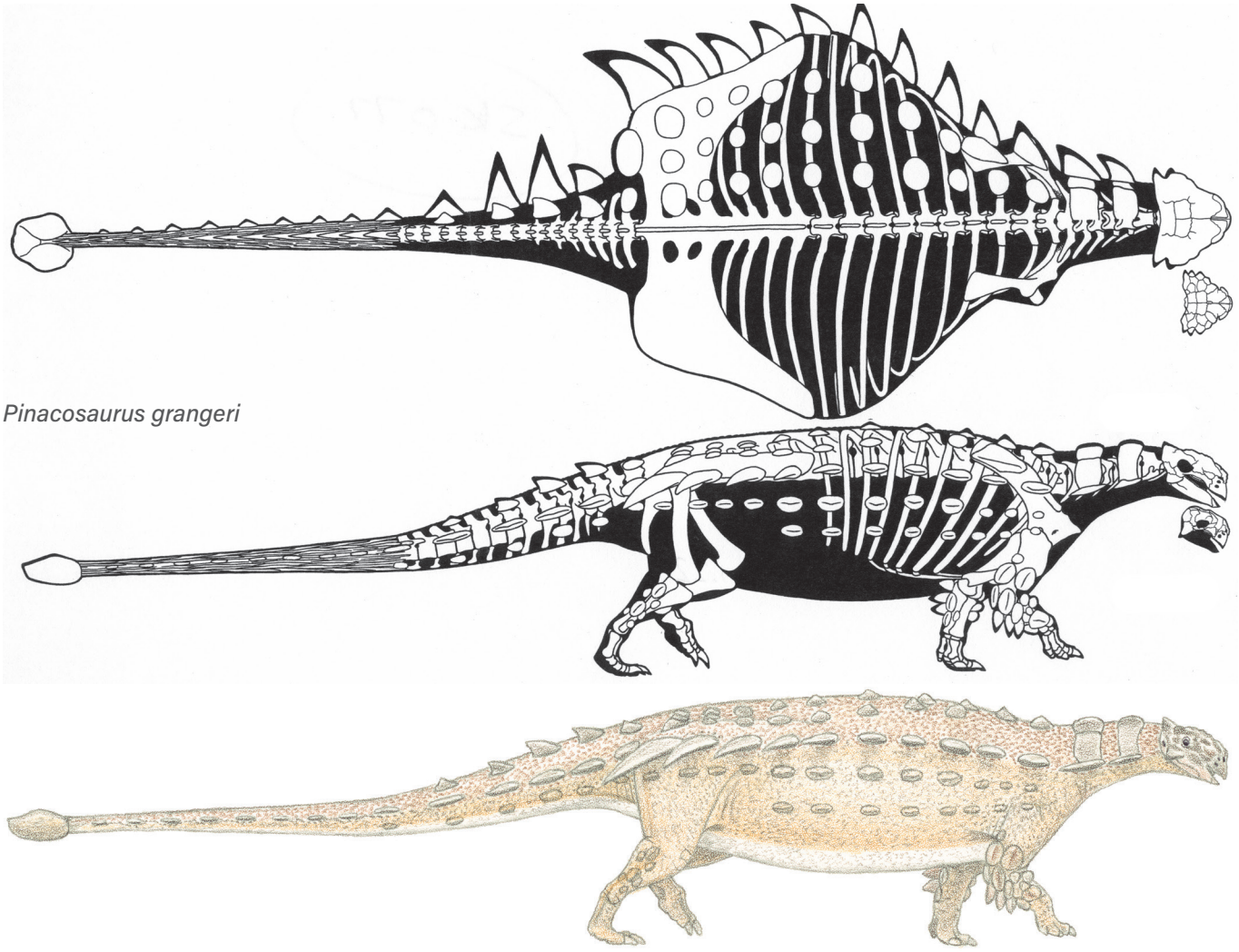
ANATOMICAL CHARACTERISTICS Head very small, nostrils with multiple exits on side of snout, upper beak broad and squared off. Short spines along flanks of trunk including hip, arm heavily armored, tail club small, subcircular in top view.

AGE Late Cretaceous, middle Campanian.

DISTRIBUTION AND FORMATION/S Mongolia, northern China?; lower Djadokhta, Wulansuhai?

HABITAT/S Desert with dunes and oases.

HABITS Probably grazed on ground cover along watercourses and at oases. Small club was high-velocity weapon for use on the small theropods of the habitat. Larynx complex indicates birdlike vocal capabilities.

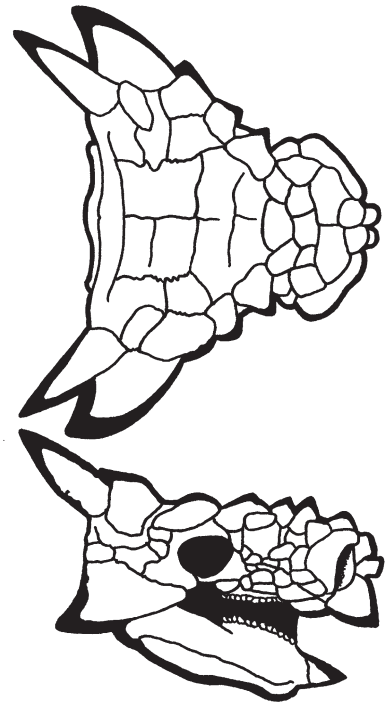


Pinacosaurus grangeri

A group of six juveniles buried at the same time by sand slide indicates they formed pods.
NOTES May include Chinese *P. mephistocephalus* as a male of the species. Preserved voice box so far unique for dinosaurs. Habitat/s probably lacked theropods large enough to attack adult *Pinacosaurus*.

Minotaurasaurus ramachandrani

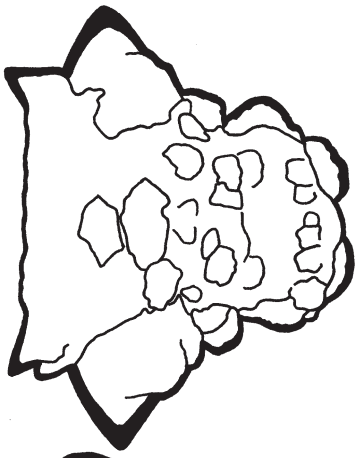
— Adult size uncertain
FOSSIL REMAINS Two skulls and minority of skeleton, probably immature.
ANATOMICAL CHARACTERISTICS Upper beak broad and squared off, skull hornlets very spiky, especially upper and lower temporal.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.
HABITAT/S Desert with dunes and oases.
HABITS Probably grazed on ground cover along watercourses and at oases.
NOTES Habitat/s probably lacked theropods large enough to attack adult *Minotaurasaurus*.



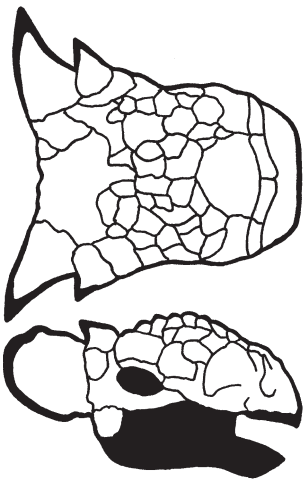
Minotaurasaurus ramachandrani

Nodocephalosaurus kirtlandensis
— 4.5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Skull.
ANATOMICAL CHARACTERISTICS Bulbous osteoderms on snout, upper temporal hornlet small, lower temporal hornlet large and forward arced.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S New Mexico; lower Kirtland.

Nodocephalosaurus kirtlandensis



Akainacephalus johnsoni



Ziapelta sanjuanensis

HABITAT/S Moderately watered floodplain woodlands, coastal swamps and marshes.
NOTES More similar to Asian than to other American ankylosaurids.

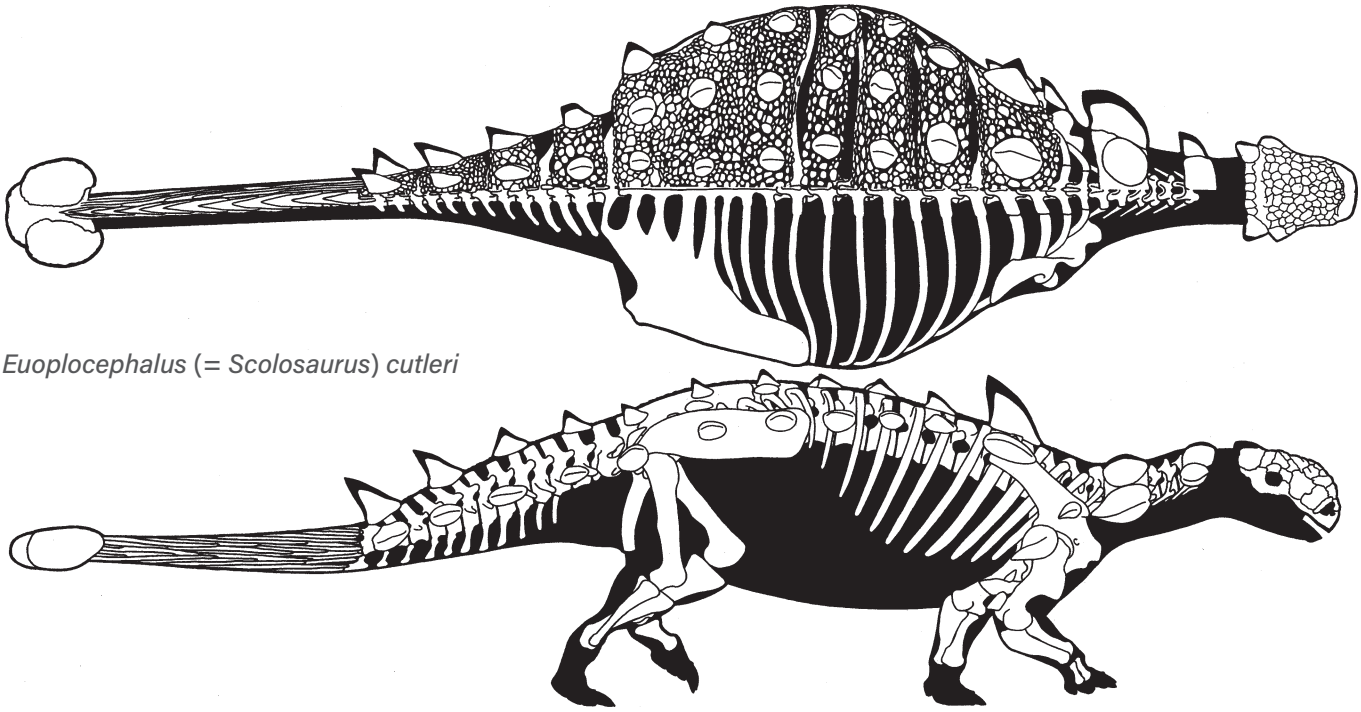
Akainacephalus johnsoni
— Adult size uncertain
FOSSIL REMAINS Skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Head deep, upper beak broad and squared off, paired snout hornlets prominent, upper temporal hornlet small, lower temporal hornlet very large. Tail club broad in top view.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Utah; lower Kaiparowitz.
HABITAT/S Moderately watered floodplain woodlands, coastal swamps and marshes.

Aletopelta coombsi
— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S California; Point Loma.
HABITAT/S Found as drift in nearshore marine sediments near rugged terrain.

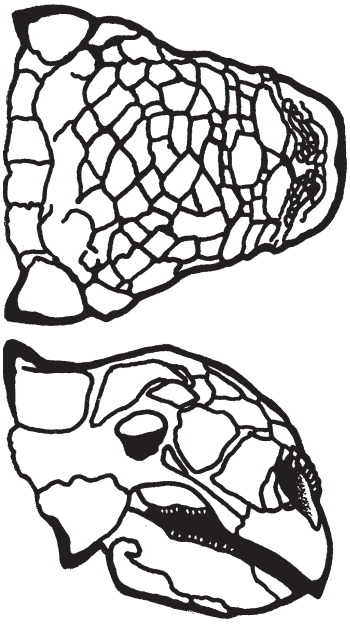
Ziapelta sanjuanensis
— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of skull and small minority of skeleton.
ANATOMICAL CHARACTERISTICS Supraorbital hornlet large, upper temporal hornlet extremely prominent, lower temporal hornlet small.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; upper Kirtland.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and possibly drier upland woodlands.

Euoplocephalus (= *Scolosaurus*) *cutleri*
— 5.6 m (18 ft) TL, 2.5 tonnes
FOSSIL REMAINS Complete and partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Upper and lower temporal hornlets large, latter more so. Short spines on forequarters and base of tail.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Oldman and/or lowermost Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and possibly drier upland woodlands.

NOTES Variations due to gender, growth, individuality, and preservation, especially flattening of skulls and varying completeness of fossils, make it difficult to determine relationships of ankylosaurine fossils from the same stratigraphic levels of western North America. Immature *Dyoplosaurus acutosquameus* and *Platypelta coombsi* may be this species. May be direct ancestor of *E.tutus*.



Euoplocephalus (= *Scolosaurus*) *cutleri*



Euoplocephalus tutus

Euoplocephalus tutus

— 5.5 m (17) TL, 2.3 tonnes

FOSSIL REMAINS Partial skulls and skeletons.

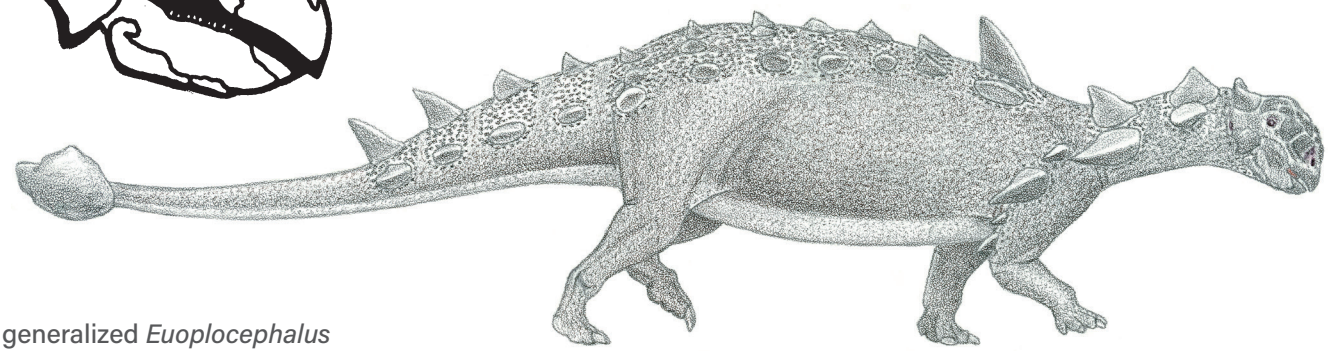
ANATOMICAL CHARACTERISTICS Supraorbital hornlet sometimes large, upper and lower temporal hornlets large, latter more so.

AGE Late Cretaceous, late middle and early late? Campanian.

DISTRIBUTION AND FORMATION/S Alberta; lower and perhaps middle Dinosaur Park.

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and possibly drier upland woodlands.

NOTES May include *Anodontosaurus inceptus*, which is not likely to be in same genus as much later *A. lambei* and *Scolosaurus thronus*; latter might be a later species.



generalized *Euoplocephalus*

Euoplocephalus

Oohkotokia (or *Zuul*) *crurivastator*

— 5 m (16 ft) TL, 2 tonnes

FOSSIL REMAINS Skull and majority of skeleton with armor in place, other possible remains.

ANATOMICAL CHARACTERISTICS Upper beak squared off, upper and lower temporal hornlets prominent and subequal in size, former project strongly backward. Tail club moderate in size, suboval, longer than wide in top view.

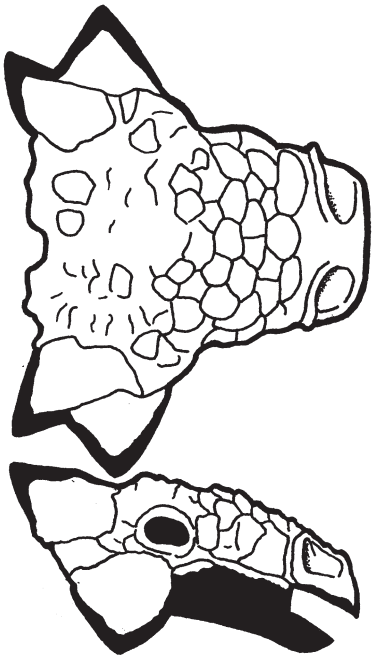
AGE Late Cretaceous, late middle and/or early late Campanian.

DISTRIBUTION AND FORMATION/S Montana; upper Judith River.

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and possibly drier upland woodlands.
HABITS Grazed ground cover.
NOTES Most of skeleton not yet described.

Oohkotokia horneri

— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Upper and lower temporal hornlets very prominent and subequal in size, former project strongly backward. Tail club subcircular in top view.



Oohkotokia (or *Zuul*) *crurivastator*

AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.

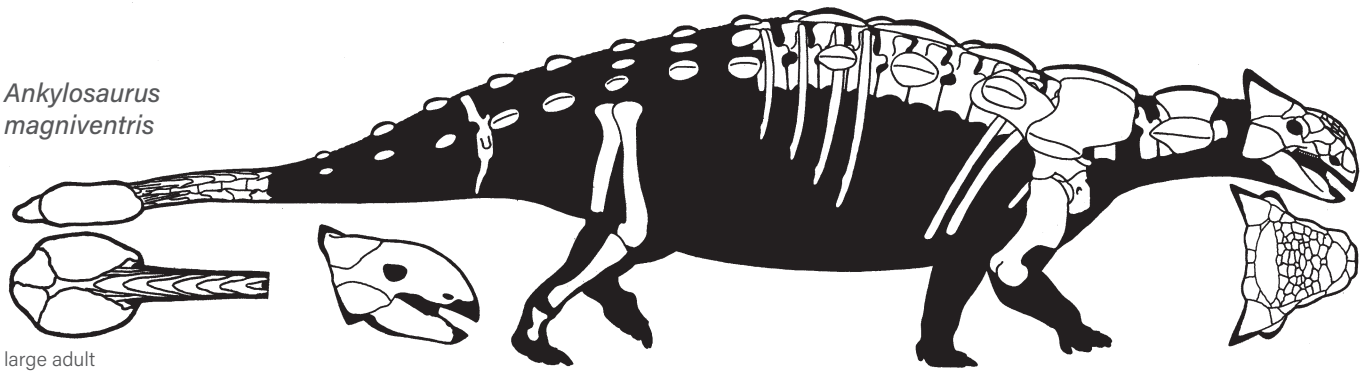
Anodontosaurus lambei

— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Several mostly complete and partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS. UPPER AND LOWER TEMPORAL HORNLETS LARGE, LATTER MORE SO. TAIL CLUB LARGE AND VERY BROAD IN TOP VIEW.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Ankylosaurus magniventris

— 7.5 m (25 ft) TL, 9 tonnes
FOSSIL REMAINS Several skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS Nostrils on side of snout, upper and lower temporal hornlets very prominent and subequal in size, former project strongly backward. Tail rather short, club large, not broad in top view.
AGE Late Cretaceous, late/latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Wyoming, Montana, Alberta; middle and/or upper Lance and Hell Creek, Scollard.
HABITAT/S Well-watered coastal woodlands.
NOTES May be more than one stratigraphic species.

Anodontosaurus lambei



Ankylosaurus magniventris

large adult

— HETERODONTOSAURIFORMES

SMALL TO GIGANTIC GENASAUR ORNITHISCHIANS OF THE EARLY JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS Very variable. Large jugal boss on cheeks, beaks narrow. Arms and legs flexed and able to run.
HABITS Low- to medium-level browsers. Defense included running and aggressive combat.
NOTES This very large group is valid only if heterodontosaurids are close relatives of marginocephalians.

— HETERODONTOSAURIDS

SMALL HETERODONTOSAURIFORMES OF THE JURASSIC OF AFRICA, EURASIA, AND THE AMERICAS.

ANATOMICAL CHARACTERISTICS Highly uniform. Heads modest sized, fairly deep, subtriangular, three teeth under upper beaks, teeth in main rows large and chisel shaped, large eyes shaded by overhanging rim. Necks fairly long and flexible. Bellies and hips fairly narrow. Trunks and tails stiffened by ossified tendons. Narrow ossified paired sternal plates connected to ribs by broad ossified sternal ribs, gastralia present in at least some taxa. Tails long. Bipedal and semiquadrupedal. Arms and hands fairly long, three of the grasping fingers tipped with large claws. Legs long, flexed, and gracile so speed potential high, toes long and tipped with blunt claws. Much or most of body covered by long, hollow fibers.
HABITS Able to consume coarse vegetation, omnivores in that also hunted small vertebrates and scavenged. Significant climbing ability. Main defense high speed, also biting with beaks and fangs. Jugal bosses on cheeks for combat and/or display within species. Longer dorsal fibers for display, shorter for insulation. Competent surface swimmers so able to cross large bodies of water, some diving ability.
NOTES Relationships of heterodontosaurids uncertain; they have been considered a distinct group at the base of ornithischians (but they have a more sophisticated form), or ornithopods (but they lack key attributes), or close to marginocephalians in general or to pachycephalosaurs, psittacosaurs, etc., in particular; the cheek boss and chisel teeth favor the latter possibilities. In any case, they show that sophisticated ornithischians had evolved by early Jurassic. Only ornithischians known to have gastralia; sternals and sternal ribs also atypical, so respiration may have been specialized compared to other ornithischians. Closest living analogues kangaroos and small, tusked deer and antelope. Whether very Early Cretaceous *Echinodon becklesii*, based on inadequate remains from England, is a heterodontosaurid is uncertain.

Heterodontosaurus tucki

— 1.2 m (4 ft) TL, 4.2 kg (9 lb)
FOSSIL REMAINS Several complete and partial skulls and a complete skeleton, juvenile to adult.
ANATOMICAL CHARACTERISTICS Short fangs in front of main tooth rows in at least one gender.
AGE Early Jurassic, late Hettangian or Sinemurian.
DISTRIBUTION AND FORMATION/S South Africa; upper Elliot.
HABITAT/S Arid.
HABITS Fangs may have been limited to males, probably used for combat within species and for defense against predators.
NOTES Probably includes the smaller, tuskless *Abrictosaurus consors* as well as *Lycorhinus angustidens*.

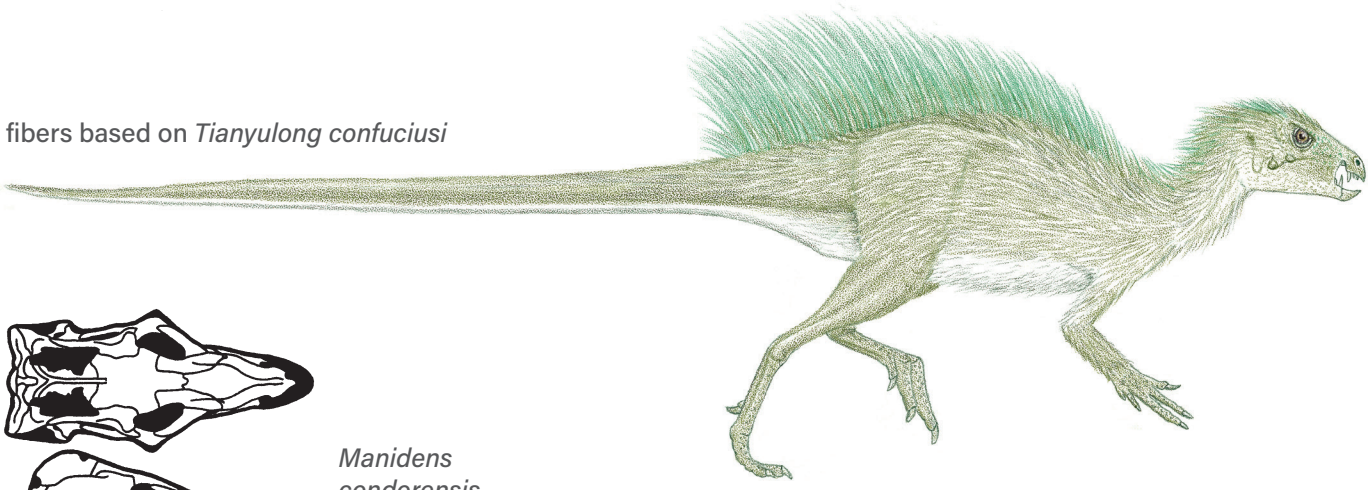
Manidens condorensis

— 0.6 m (2 ft) TL, 0.5 kg (1.8 lb)
FOSSIL REMAINS Minority of skeleton, other possible partial remains.
ANATOMICAL CHARACTERISTICS Toes may be exceptionally long and slender.
AGE Early Jurassic, late Toarcian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Cañadón Asfalto.
HABITS Toes indicate was both a fast runner and good climber.
NOTES Not certain whether foot belongs to species. If adult, the smallest known ornithischian.

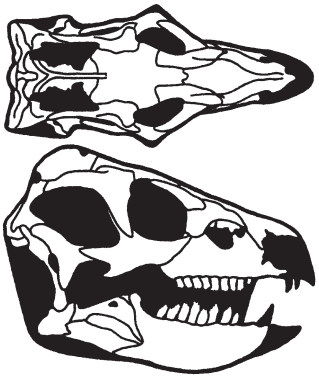
Tianyulong confuciusi

— Adult size uncertain
FOSSIL REMAINS Partial skull and skeletons with external fibers, subadult.
ANATOMICAL CHARACTERISTICS Short fangs in front of main tooth rows. Fibers dense, thick, and very long over trunk and especially tail.
AGE Late Jurassic, middle Oxfordian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Tiaojishan.

Heterodontosaurus tucki



fibers based on *Tianyulong confuciusi*



Manidens condorensis

HABITAT/S Well-watered forests and lakes, winters chilly with snow.
NOTES This fossil shows that at least some small ornithischians bore external fibers and that such body coverings evolved early in the group. Originally thought to be from Cretaceous Yixian Formation.

Fruitadens haagarorum

— 0.75 m (2.5 ft) TL, 0.1 kg (2 lb)
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Short fang in front of lower tooth row.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Colorado; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

— MARGINOCEPHALIANS

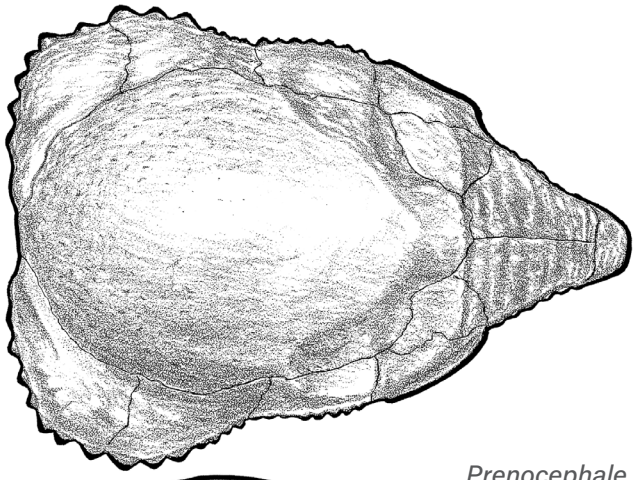
SMALL TO GIGANTIC HETERODONTOSAURIFORM ORNITHISCHIANS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

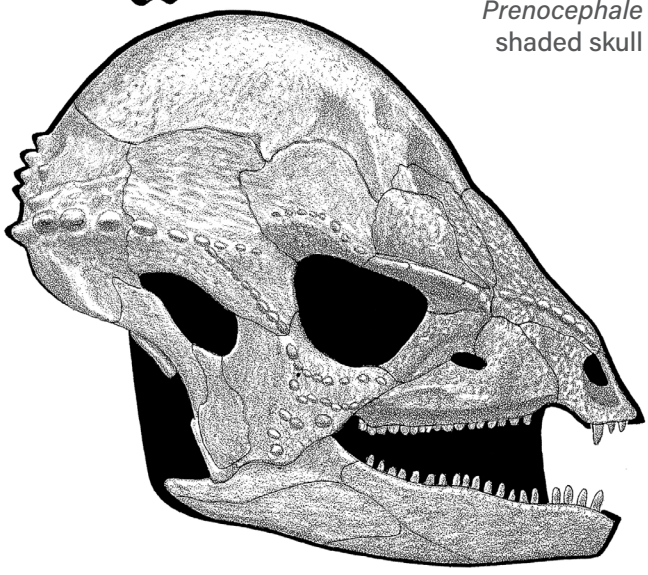
ANATOMICAL CHARACTERISTICS Very variable. Heads large, heavily constructed, back of heads broad, forming at least incipient crest, beaks narrow, eyes not very large. Tails long to fairly short. Fully bipedal to quadrupedal, arms and legs flexed and able to run. Fingers five to three, tipped with small blunt claws or hooves. Legs not gracile, so speed potential moderate, four long toes.
HABITS Low- to medium-level browsers. Defense included running and aggressive combat. Large-headed, heavy-boned bodies too dense for ready surface swimming, ability to cross large bodies of water correspondingly limited.

— PACHYCEPHALOSAURIDS

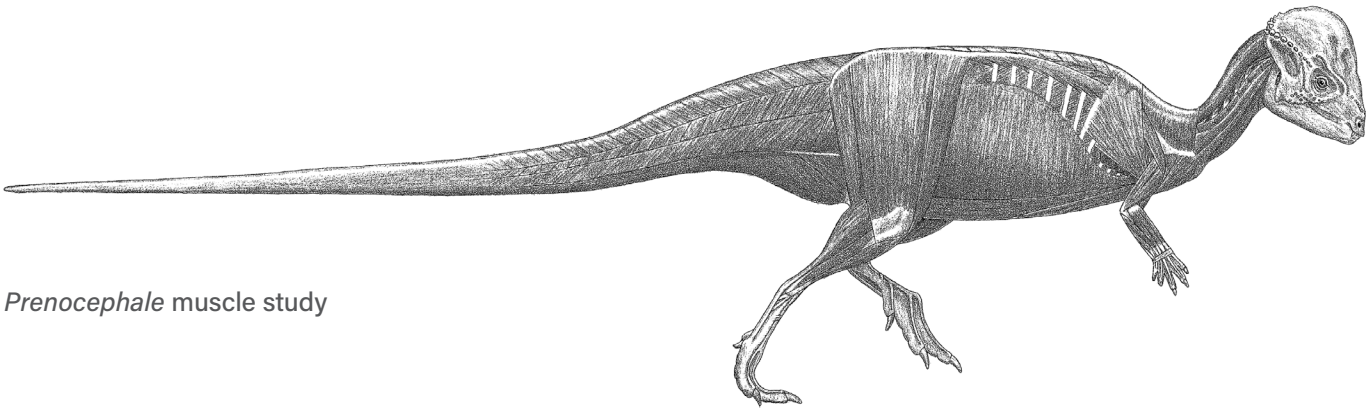
SMALL TO MEDIUM-SIZED MARGINOCEPHALIANS OF THE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads deep, massively constructed, beaks small, skull roofs thickened, may be domed in all adults, domes may be better developed in males in at least some species; adorned with rows of small hornlets, teeth under upper beaks, main tooth rows short, teeth small. Vertebrae heavily constructed. Trunks fairly long. Bellies, hips, and tail bases very broad to accommodate enlarged bellies. Tails long, bases sweep down from hips, last two-thirds stiffened by a dense basket-weave lattice of ossified tendons. Fully bipedal. Arms and hands small, five grasping fingers tipped with small blunt claws. Four long toes tipped with blunt claws.
HABITAT/S Variable, from semiarid to well-watered forests.
HABITS Defense included running and possible headbutting. Males may have used domes for competitive displays. May have butted flanks of competitors and predators, high-speed head-to-head butting unlikely because of lack of broad impact surface to provide stability.
NOTES Pachycephalosaurids are sometimes segregated into two groups, flat headed and dome headed, but it is probable that the former are immature examples of the dome-headed group, or females.





Prenocephale shaded skull



Prenocephale muscle study

Stenopelix valdensis
— 1.4 m (4.5 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Tail base not as broad as in other pachycephalosaurs.
AGE Early Cretaceous, Berriasian.
DISTRIBUTION AND FORMATION/S Central Germany; Obernkirchen Sandstein.

Wannanosaurus yansiensis
— Adult size uncertain
FOSSIL REMAINS Majority of skull and minority of skeleton, probably immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Xiaoyan.
NOTES Probably an immature fossil.

Goyocephale (or *Stegoceras*) *lattimorei*
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Cretaceous, late Santonian and/or early Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; unnamed formation.
HABITAT/S Well-watered woodland with seasonal rain.

Foraminacephale brevis
— 1.5 m (5 ft) TL, 12 kg (25 lb)
FOSSIL REMAINS Skull domes.
ANATOMICAL CHARACTERISTICS Head not heavily adorned.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; Dinosaur Park, Oldman.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May include *Colepiocephale lambei* and *Gravitholus albertae.*

Stegoceras validum
— 2.2 m (7 ft) TL, 40 kg (80 lb)
FOSSIL REMAINS Skull domes, possibly complete skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head not heavily adorned, three teeth under upper beak.
AGE Late Cretaceous, late middle and early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower and middle Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

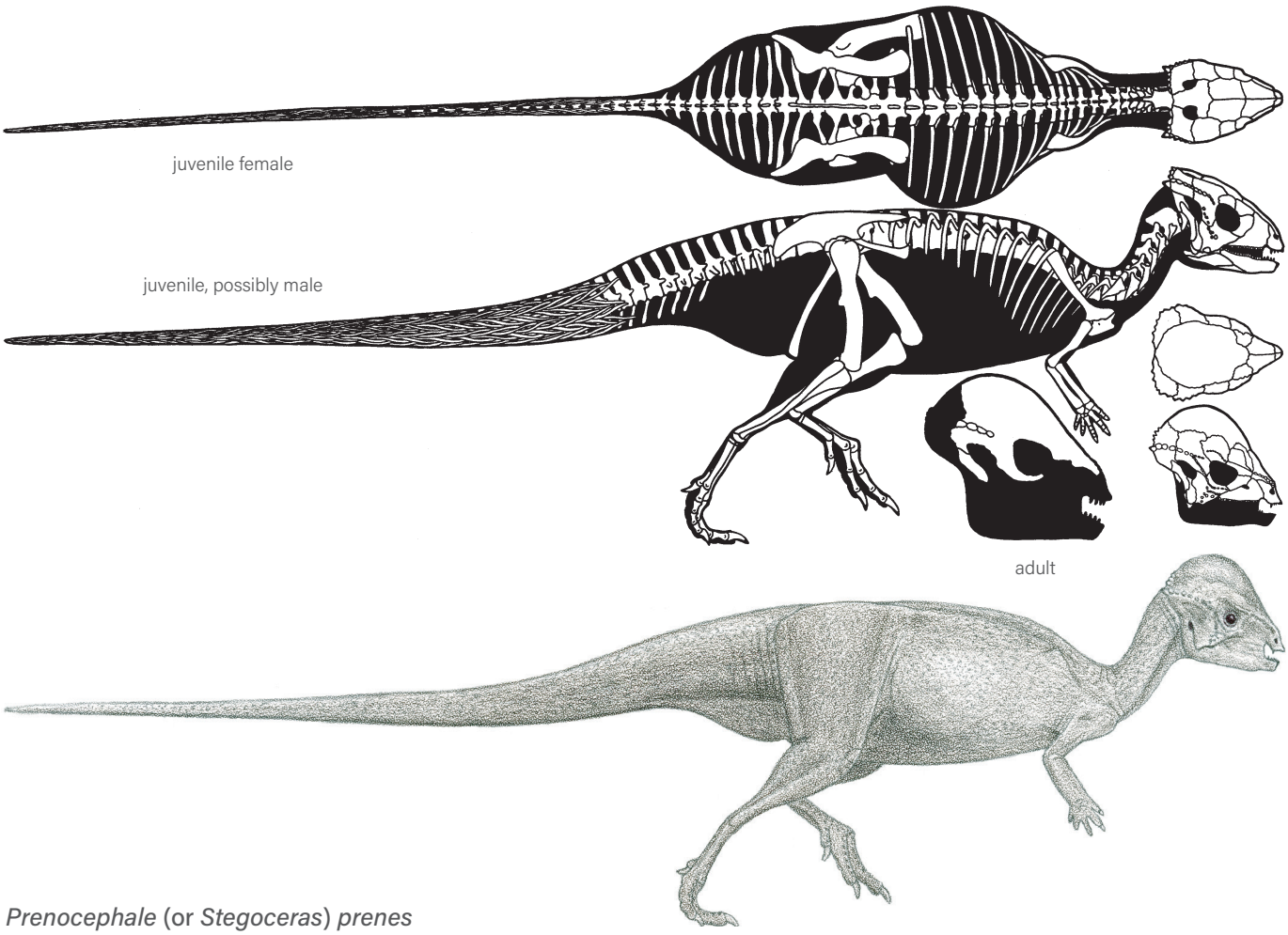
Stegoceras validum

NOTES Because of inadequate remains, and because the level of many fossils is uncertain, it is possible that more than one species existed; may include *Hanssuesia sternbergi*, which may be a gender morph, probably not present earlier or later than Dinosaur Park Formation.

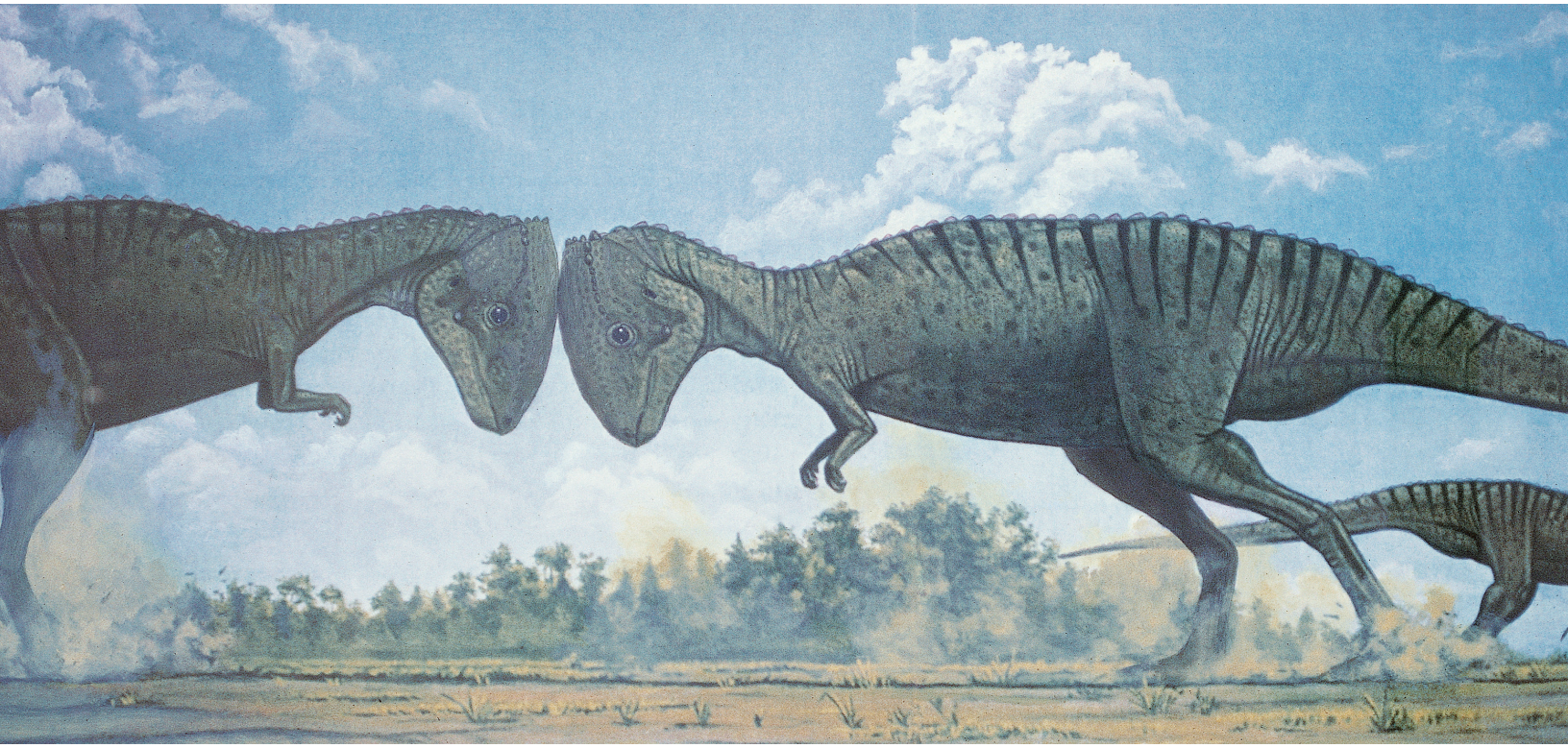
Stegoceras? *edmontonensis*
— 2 m (6.5 ft) TL, 40 kg (80 lb)
FOSSIL REMAINS Skull domes.
ANATOMICAL CHARACTERISTICS Head not heavily adorned.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Tylocephale (or *Stegoceras*) *gilmorei*
— 2 m (6.5 ft) TL, 40 kg (80 lb)
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.

Prenocephale (or *Stegoceras*) *prenes*
— 3 m (10 ft) TL, 100 kg (200 lb)
FOSSIL REMAINS Complete skull with minority of skeleton.



Prenocephale (or *Stegoceras*) *prenes*



ANATOMICAL CHARACTERISTICS Head not heavily adorned, three teeth under upper beak.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
NOTES Flat-headed *Homalocephale calathocercos* may be immature female of *P. prenes*.

Pachycephalosaurus wyomingensis

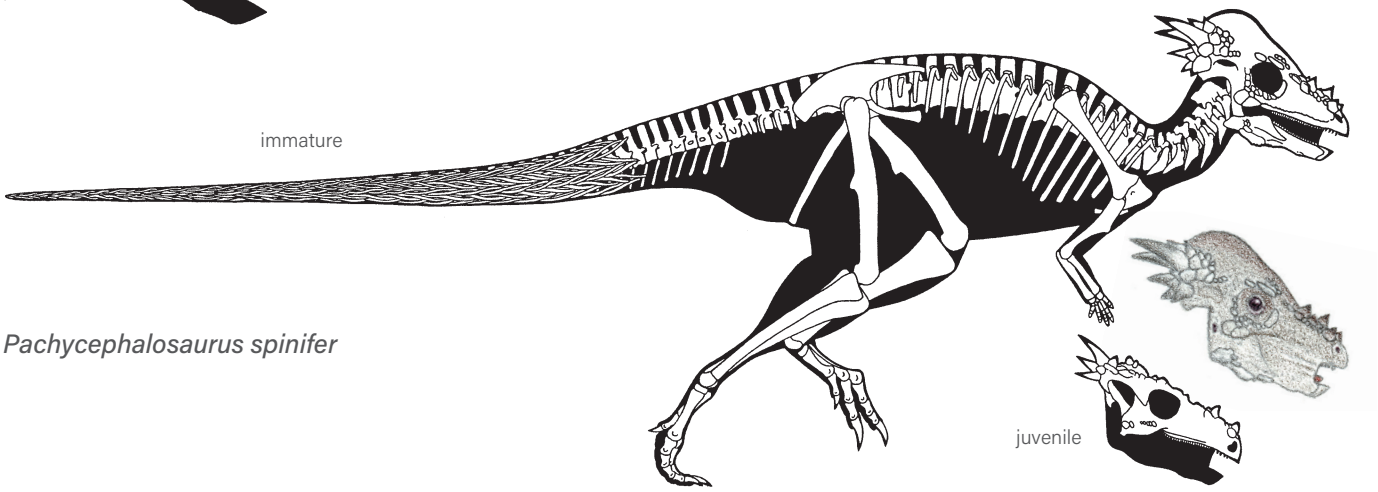
— 4.5 m (15 ft) TL, 400 kg (900 lb)
FOSSIL REMAINS Skull and partial skulls.

Pachycephalosaurus wyomingensis

ANATOMICAL CHARACTERISTICS Arrays of modest-sized spikes on snout and back of head.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Montana, South Dakota, Wyoming; lower Lance and Hell Creek.
HABITAT/S Well-watered coastal woodlands.

Pachycephalosaurus spinifer

— Adult size uncertain
FOSSIL REMAINS Skull and majority of skeleton possibly immature, juvenile skull.
ANATOMICAL CHARACTERISTICS Array of modest-sized spikes on snout, large spikes on back of head in at least some adults, four teeth under upper beak.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Montana, South Dakota, Wyoming, Saskatchewan; middle Lance and Hell Creek.
HABITAT/S Well-watered coastal woodlands.
NOTES Originally in genus *Stygimoloch*, but only major difference from *P. wyomingensis* is larger head spikes. *Dracorex hogwartsia* is a juvenile of this species, which is not a juvenile of earlier *P. wyomingensis*.



Pachycephalosaurus spinifer

— CERATOPSIANS

SMALL TO GIGANTIC MARGINOCEPHALIANS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA OF NORTH AMERICA AND ASIA.

ANATOMICAL CHARACTERISTICS Variable. Upper beaks set on rostral bone, teeth in main tooth rows form cutting and slicing edges.
HABITAT/S Very variable, from deserts to well-watered forests.
HABITS Omnivores in that also hunted small vertebrates and/or scavenged. Defense included biting. Very fragmentary, Early Cretaceous *Serendipaceratops arthurcclarkei* from Australia may indicate group's presence in Southern Hemisphere.

— CHAOYANGSAURIDS

SMALL CERATOPSIANS LIMITED TO THE LATE JURASSIC OF ASIA.

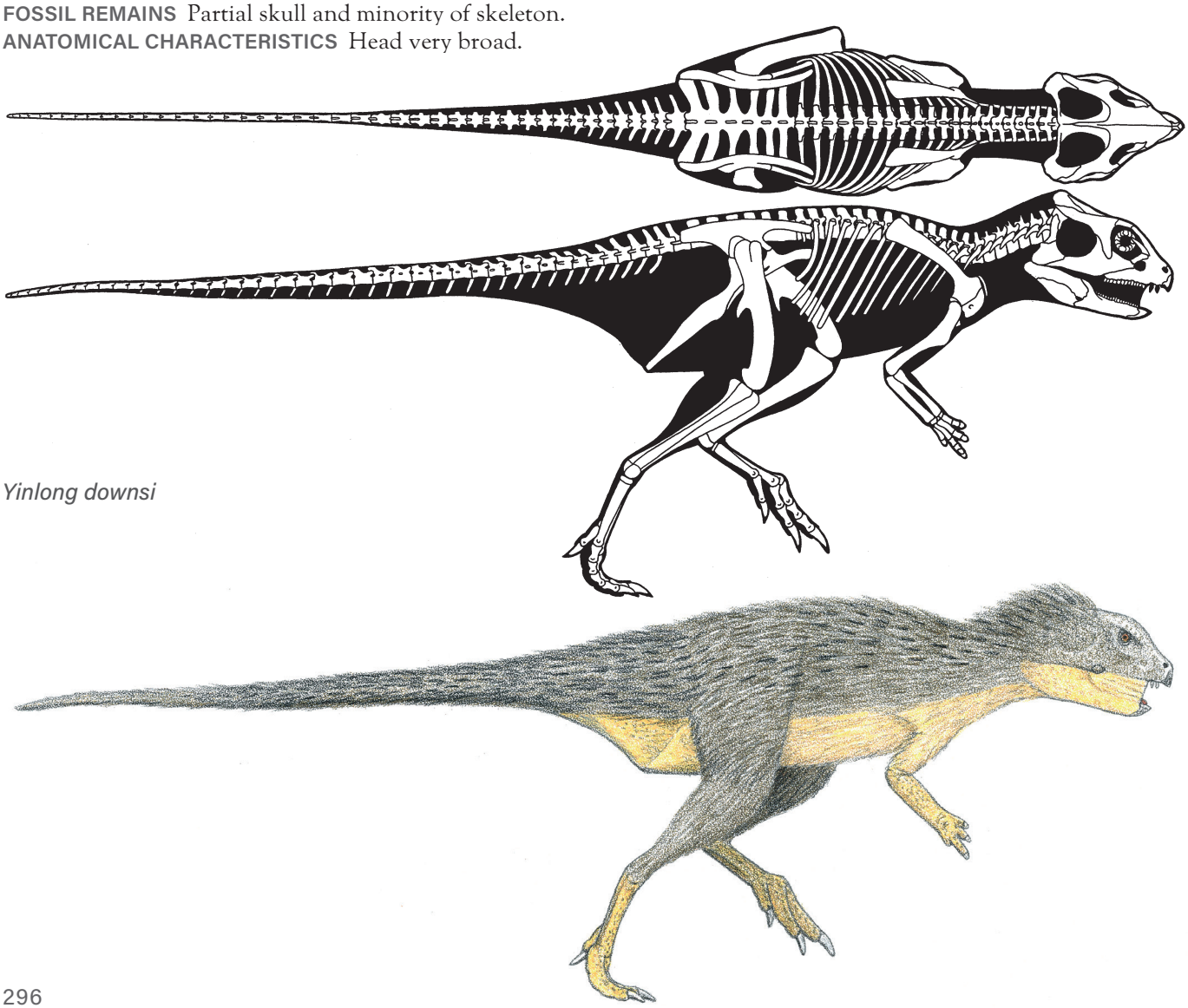
ANATOMICAL CHARACTERISTICS Heads large, deep, and broad because temporal region is large, heavily built, eyes shaded by overhanging rim, beaks small, slightly hooked, first two upper teeth are fangs, teeth in main rows chisel

shaped. Necks short and stout. Bellies and hips broad in at least some examples. Trunks stiffened by ossified tendons. Bipedal except could move quadrupedally at slow speeds because arms are short, grasping fingers tipped with small blunt claws. Main toes long and tipped with blunt claws.
HABITS Defense included biting with beaks and fangs.

Yinlong downsi
— 1.6 m (5.2 ft) TL, 20 kg (40 lb)
FOSSIL REMAINS A number of skulls and skeletons of varying completeness.
ANATOMICAL CHARACTERISTICS Head strongly triangular in side and top views. Leg long, heavily built.
AGE Late Jurassic, early Oxfordian.
DISTRIBUTION AND FORMATION/S Northwestern China; upper Shishugou.
NOTES Preservational and photographic distortions and proportional differences leave proportions of restoration somewhat uncertain. May include *Hualianceratops wucaiwanensis* at least in genus, otherwise the earliest known ceratopsian.

Chaoyangsaurus youngi
— 1 m (3 ft) TL, 5 kg (10 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head very broad.
AGE Late Jurassic, Tithonian.
DISTRIBUTION AND FORMATION/S Northeastern China; Tuchengzi.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.

Xuanhuaceratops niei
— 1 m (3 ft) TL, 5 kg (10 lb)
FOSSIL REMAINS Several partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Probably Late Jurassic.
DISTRIBUTION AND FORMATION/S Northeastern China; Houcheng.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.



Yinlong downsi

— PAXCERATOPSIANS

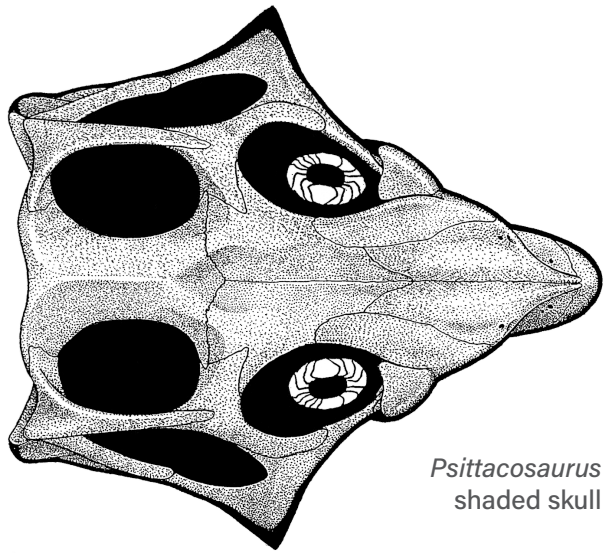
SMALL TO GIGANTIC CERATOPSIANS OF THE CRETACEOUS OF NORTH AMERICA AND ASIA.

ANATOMICAL CHARACTERISTICS Variable. Heads deep, massively constructed, beaks deep, usually parrot shaped, jugal bosses very large, teeth in main tooth rows form cutting edges. Skin consists of large, rosette-pattern scales.
HABITAT/S Very variable, from deserts to well-watered forests.
HABITS Able to consume coarse vegetation, omnivores in that also hunted small vertebrates and/or scavenged with parrot beaks and slicing teeth. Defense included running, biting with beaks.
NOTES Ceratopsians including psittacosaurs and neoceratopsians and their common ancestor, including *Triceratops*.

— PSITTACOSAURIDS

CERATOPSIANS LIMITED TO THE EARLY CRETACEOUS OF ASIA.

ANATOMICAL CHARACTERISTICS Highly uniform. Heads extremely broad, beaks not hooked, nostrils small, jugal bosses exceptionally large, eyes facing partly upward, lower jaws very deep with flange on lower rim, no teeth under upper beaks, main tooth rows short, teeth chisel shaped. Tails fairly long. Bipedal except could move quadrupedally at slow speeds. Arms short, three grasping fingers tipped with small blunt claws. Toes long and tipped with blunt claws. Long bristle fibers atop at least tails in at least some species. Gizzard stone bundles present.
ONTOGENY Growth rates moderate.
HABITAT/S Very variable, from deserts to well-watered forests.
HABITS May have consumed hard nuts as parrots do. The unusually upward-oriented eyes may have served to spot small winged predatory avepods about to ambush from branches above.
NOTES The large number of generically similar yet specifically distinctive species in one genus, *Psittacosaurus*, sets a useful standard for other dinosaur genera.



Psittacosaurus shaded skull

Psittacosaurus? *xinjiangensis*

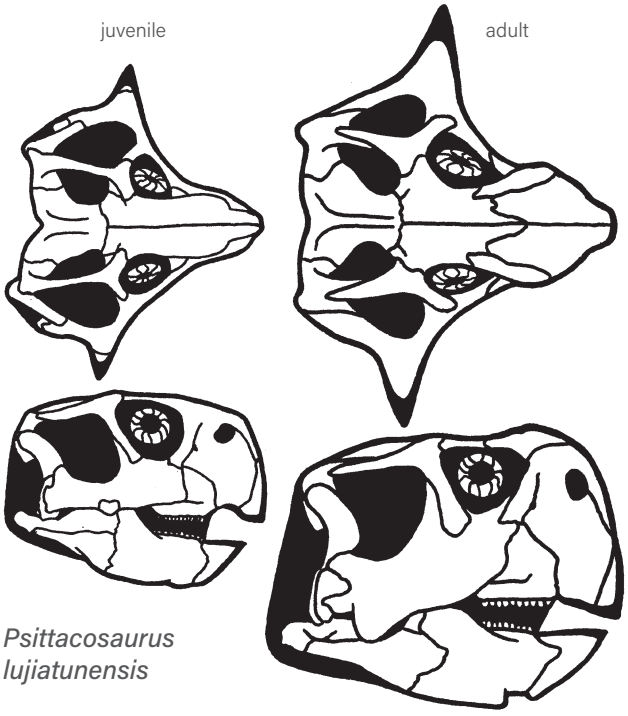
— Adult size uncertain
FOSSIL REMAINS A few skulls and skeletons of varying completeness and often damaged, one adult.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short, eyes shaded by overhanging rim.
AGE Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Northwestern China; lower Lianmuqin.
NOTES Fossils from different locations, so may not be one species, recent realization that this poorly known taxon is much earlier than later *Psittacosaurus* suggests is a different genus.

Psittacosaurus amitabha

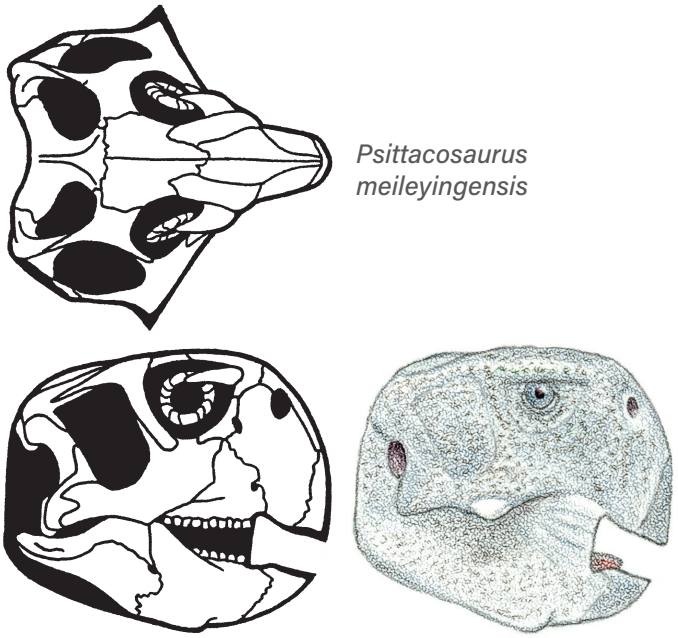
— 1.3 m (4 ft) TL, 12 kg (40 lb)
FOSSIL REMAINS Majority of damaged skull and minority of skeleton, possibly juvenile remains.
ANATOMICAL CHARACTERISTICS Head subrectangular in side view.
AGE Early Cretaceous, Barremian.
DISTRIBUTION AND FORMATION/S Mongolia; Andakhuduk.

Psittacosaurus lujiatunesis

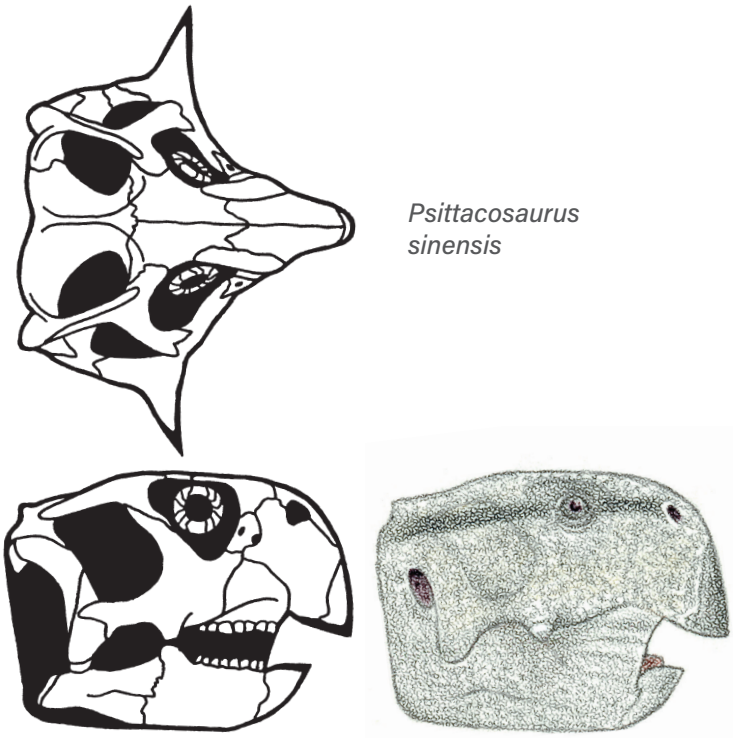
— 1.5 m (5 ft) TL, 15 kg (35 lb)
FOSSIL REMAINS Number of adult to juvenile skulls, number of juvenile skeletons.
ANATOMICAL CHARACTERISTICS Head deep, squarish.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lowermost Yixian.



Psittacosaurus lujiatunensis



Psittacosaurus meileyingensis



Psittacosaurus sinensis

HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES *Hongshanosaurus houi*, a problematic species based on a small juvenile skull, may be this species.

Psittacosaurus unnamed species?

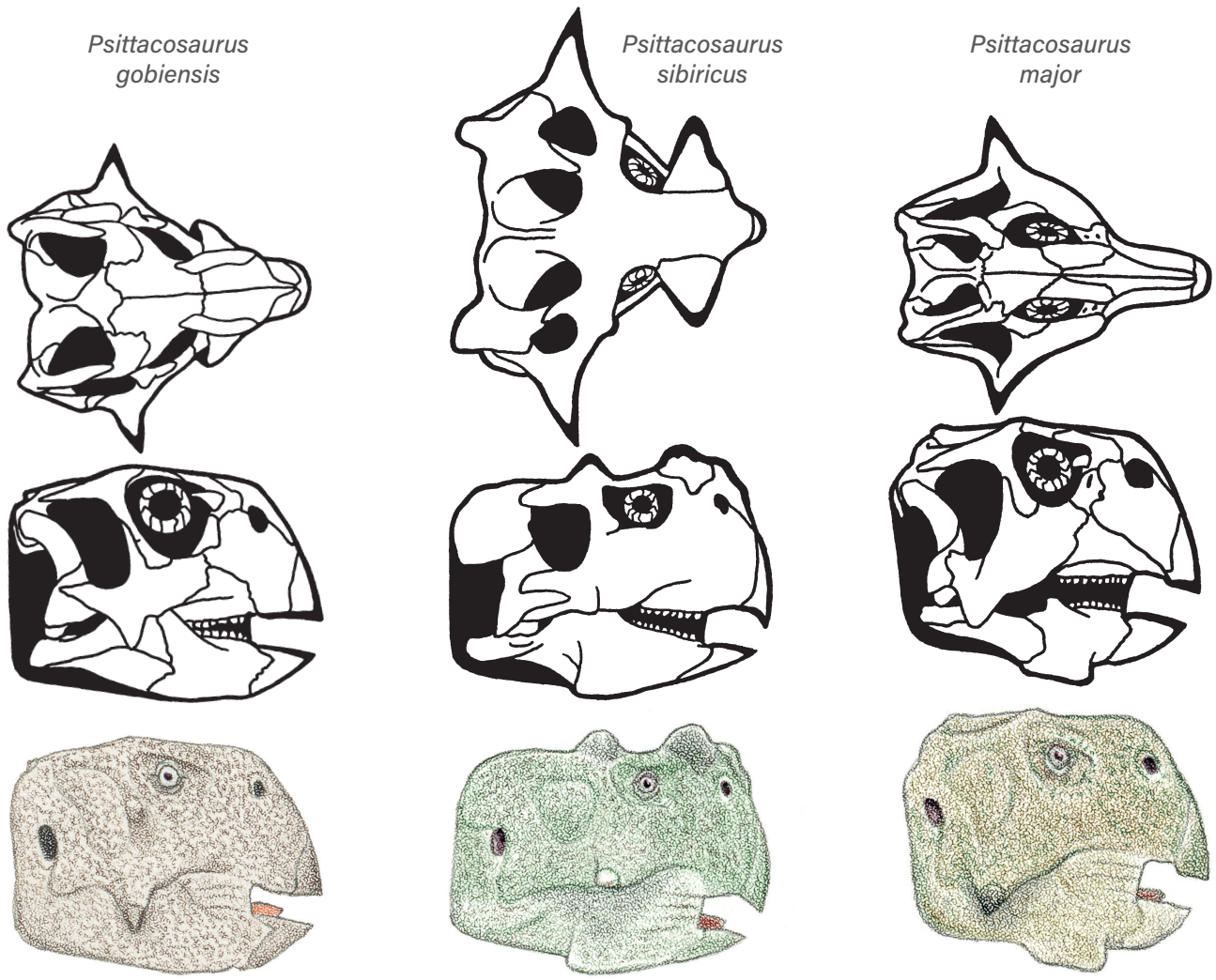
1.2 m (4 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Nearly complete distorted skull and skeleton, skin, tail bristles.
ANATOMICAL CHARACTERISTICS Larger scales on upper arm, tail adorned with long bristles.
AGE Early Cretaceous, probably early Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Original discovery not documented, probably from higher in the Yixian than *P. lujiatunensis*. May have been direct ancestor of *P. meileyingensis*.

Psittacosaurus meileyingensis

— 1.1 m (3.5 ft) TL, 8 kg (18 lb)
FOSSIL REMAINS Two complete skulls and four partial skeletons.
ANATOMICAL CHARACTERISTICS Head squarish, snout short and deep, eyes shaded by overhanging rim.
AGE Early Cretaceous, early or middle Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Jiufotang.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Psittacosaurus sinensis

— 1 m (3 ft) TL, 6 kg (13 lb)
FOSSIL REMAINS Numerous skulls and skeletons, some complete, completely known.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short, jugal bosses are large spikes.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Eastern China; Qingshan.
NOTES Probably includes *P. youngi*.



Psittacosaurus gobiensis
— 1 m (3 ft) TL, 6 kg (13 lb)
FOSSIL REMAINS Complete skull and majority of skeletons.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short, jugal bosses are large spikes, small triangular hornlet behind orbit.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Northern China; Bayan Gobi.

Psittacosaurus sibiricus
— 1.5 m (5 ft) TL, 15 kg (35 lb)
FOSSIL REMAINS Complete skull and majority of skeleton, partial remains.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short, wider than long, exceptionally deep, large projections above and forward of orbits, jugal bosses are large spikes, flange on lower jaw enlarged.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Central Siberia; Ilek.

Psittacosaurus major
— 1.6 m (5 ft) TL, 18 kg (40 lb)
FOSSIL REMAINS Complete skull and nearly complete skeleton.
ANATOMICAL CHARACTERISTICS Head exceptionally large but rather narrow, deep, subrectangular, snout short.
AGE Early Cretaceous, early Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Narrowness of the large head may have reduced its weight in this biped.

Psittacosaurus neimongoliensis
— 1.1 m (3.5 ft) TL, 8 kg (18 lb)
FOSSIL REMAINS Nearly complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short.
AGE Late Early Cretaceous.

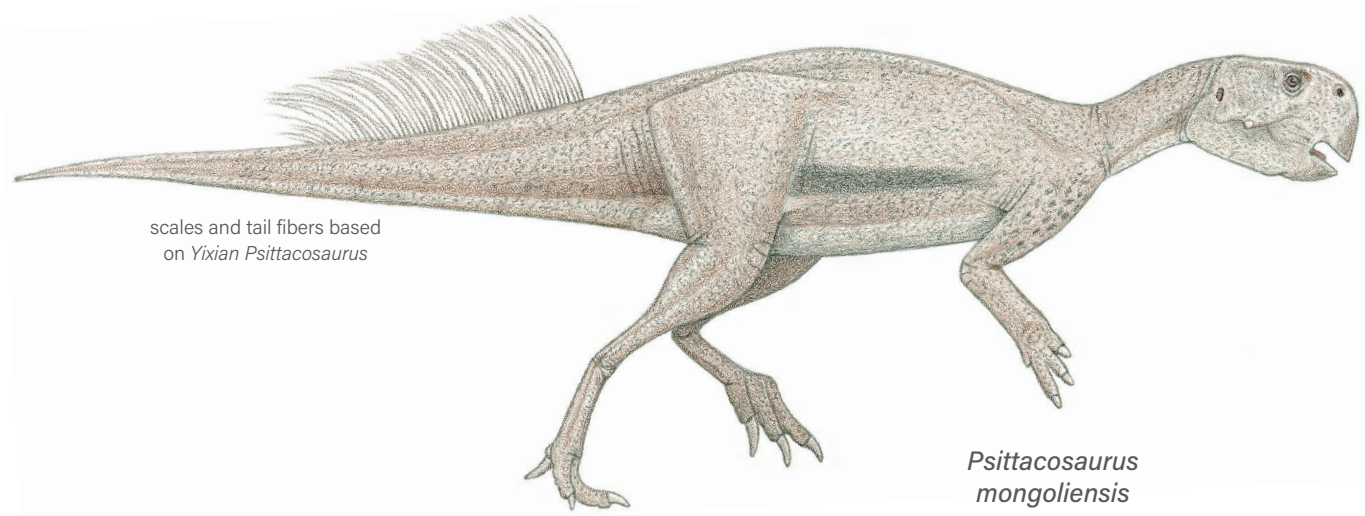
DISTRIBUTION AND FORMATION/S Northern China; Ejinhoro.
NOTES Probably includes *P. ordosensis*.

Psittacosaurus mongoliensis

— 1.5 m (5 ft) TL, 15 kg (35 lb)
FOSSIL REMAINS Dozens of skulls and skeletons, many complete, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Head subrectangular, snout short.
AGE Early Cretaceous, Aptian and/or Albian.
DISTRIBUTION AND FORMATION/S Southern Siberia, Mongolia, northern China; Khukhtekskaya Svita, Khulsyngolskaya Svita, Shestakovskaya Svita.
NOTES The classic psittacosaur.

Psittacosaurus neimongoliensis

Psittacosaurus mongoliensis



Psittacosaurus mongoliensis

Psittacosaurus mazongshanensis
— Size uncertain
FOSSIL REMAINS Nearly complete skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Snout rather long.
AGE Late Early Cretaceous.
DISTRIBUTION AND FORMATION/S Central China; lower Xinminbao Group.

— NEOCERATOPSIANS

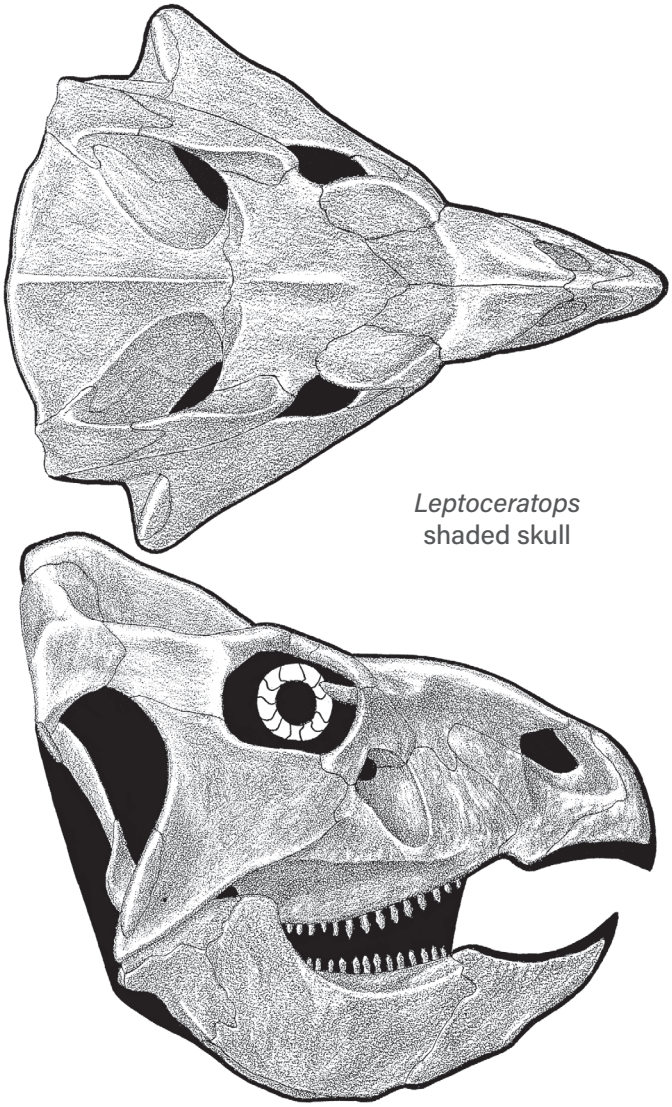
SMALL TO GIGANTIC CERATOPSIANS OF THE CRETACEOUS OF NORTH AMERICA AND ASIA.

ANATOMICAL CHARACTERISTICS Moderately variable. Heads exceptionally large, jugal bosses moved back toward jaw joint, upper beaks at least slightly hooked. Necks straight. Trunks stiffened by ossified tendons. Tails not long. Largely quadrupedal; those that were may have been able to gallop as well as trot, shoulders somewhat lower than hips. Hands and five fingers short, tipped with hooves. Toes tipped with hooves.
HABITAT/S Highly variable, from deserts to well-watered forests.
HABITS Oversized heads may have been at least in part for competitive display within species. Defense often aggressive as in suids and rhinos.

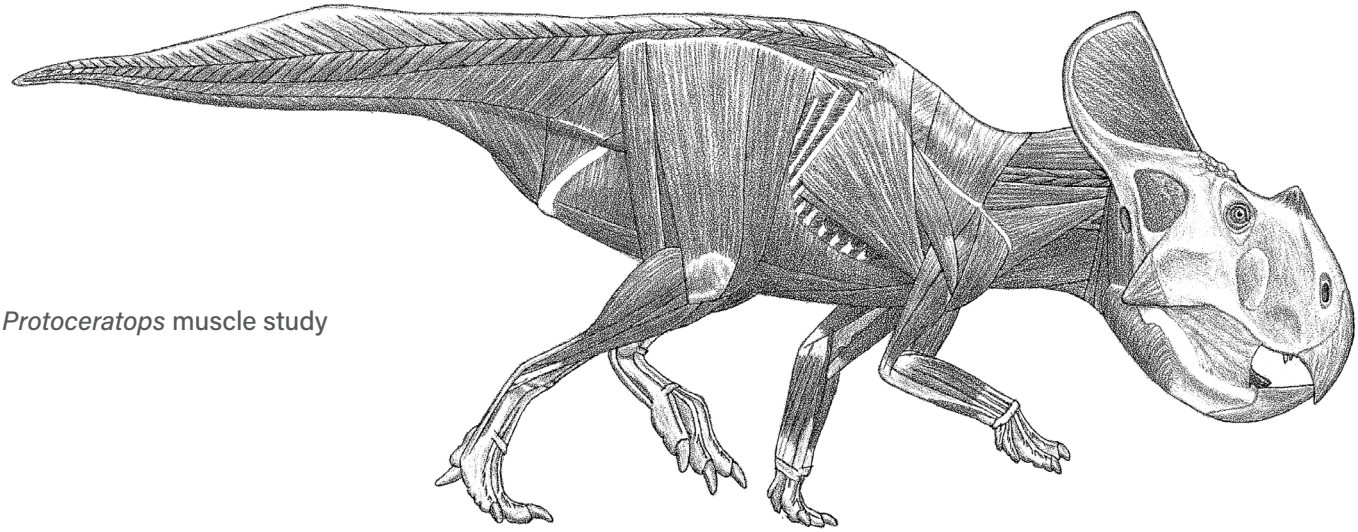
— PROTOCERATOPSIDS

SMALL TO FAIRLY LARGE NEOCERATOPSIANS OF THE CRETACEOUS OF NORTH AMERICA AND ASIA.

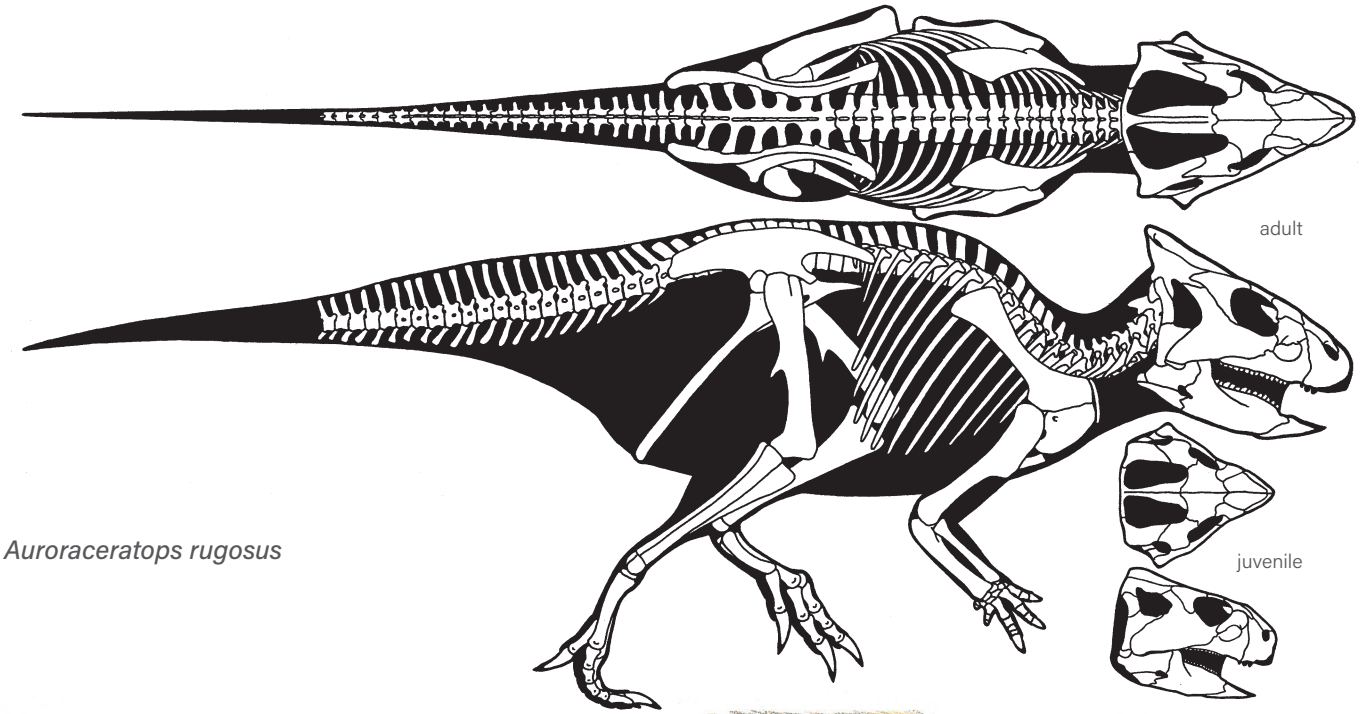
ANATOMICAL CHARACTERISTICS Nasal openings set high and not very large, teeth sometimes under upper beaks, main tooth rows short, teeth chisel shaped. Pelvic ilia horizontal. May have been able to run bipedally as well as quadrupedally. Toes long.
HABITATS Highly variable, from deserts to well-watered forests.
NOTES Group may be splittable into a number of subdivisions. Closest living analogues suids.



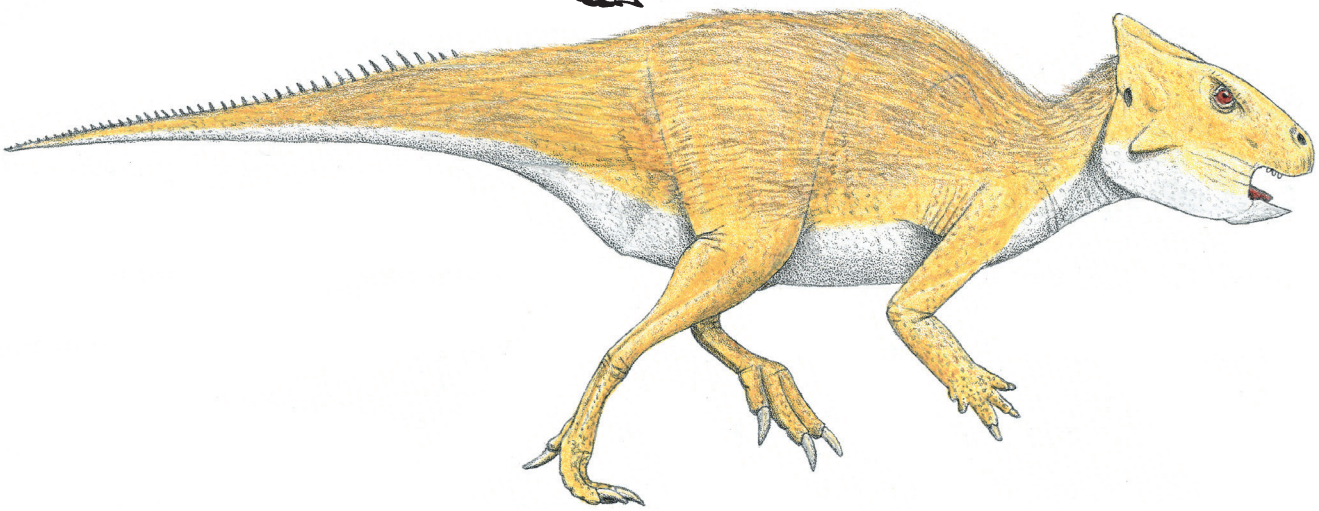
Leptoceratops
shaded skull



Protoceratops muscle study



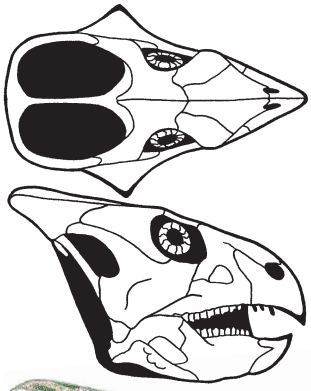
Auroraceratops rugosus



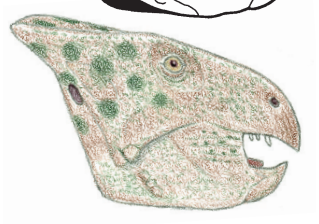
Auroraceratops rugosus
— 1.25 m (4 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Numerous skulls and skeletons, adult to juvenile.
ANATOMICAL CHARACTERISTICS Snout short, beak not hooked, frill incipient, three teeth under upper beak, lower beak sharp tipped; neck very short, front trunk vertebral series strongly downcurved and ribs long so trunk is short and deep; lower arm fairly short, central finger largest, largely bipedal.
AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Northern China; middle Xinminbao Group.
HABITS Small inner fingers and plump trunk indicate was not as adapted for digging as most other small ornithischians.
NOTES Skeletons preserved on sides show strong downcurve of trunk vertebrae, so restoration showing straighter back incorrect, as is longer neck.

Graciliceratops mongoliensis
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Head frill short, not broad. Leg long, largely bipedal.
AGE Late Cretaceous.
DISTRIBUTION AND FORMATION/S Mongolia; Shireegiin Gashuun.

Mosaiceratops azumai



Liaoceratops yanzigouensis



Beg tse
— 1 m (3 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Four teeth under upper beak.
AGE Early or Late Cretaceous, Albian or Cenomanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Ulaanoosh.
NOTES Skull is missing part of snout and frill.

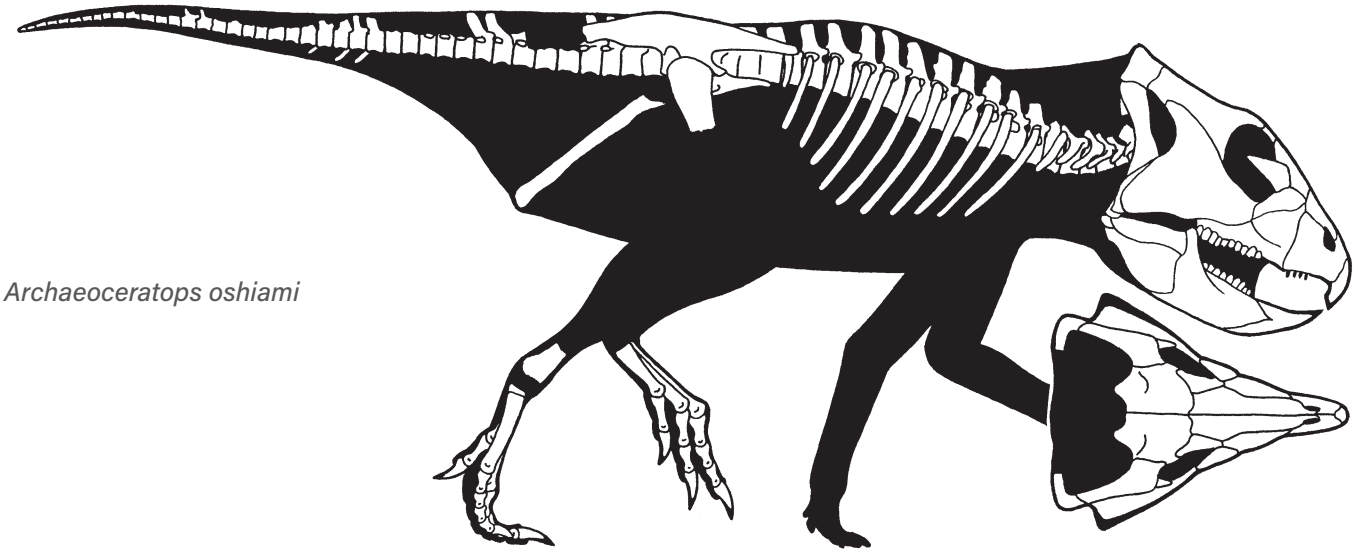
Mosaiceratops azumai
— 1 m (3 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Nearly complete skulls and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head very broad, no teeth under upper beak.
AGE Late Cretaceous, Turonian or Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Xiaguan.

Liaoceratops yanzigouensis
— 0.5 m (1.7 ft) TL, 1.5 kg (3 lb)
FOSSIL REMAINS Two skulls, juvenile and adult.
ANATOMICAL CHARACTERISTICS Head deep, frill very short and not broad, three teeth under upper beak.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Aquilops americanus
— Adult size uncertain
FOSSIL REMAINS Majority of skull, probably juvenile.
ANATOMICAL CHARACTERISTICS Three teeth under upper beak.
AGE Early Cretaceous, late Aptian to early Albian.
DISTRIBUTION AND FORMATION/S Wyoming; Cloverly.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.

Archaeoceratops oshimai
— 0.9 m (3 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Head deep, eyes shaded by overhanging rim, frill incipient, four teeth under upper beak.

Aquilops americanus



Archaeoceratops oshiami

AGE Early Cretaceous, Aptian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.
NOTES It is not known whether this is a short-armed biped or longer-armed quadruped.

Cerasinops hodgskissi

— 2.5 m (8 ft) TL, 200 kg (400 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Head deep, frill short, jaw deep. Arm short compared to hind limb, so possibly more bipedal than other protoceratopsids.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; lower Two Medicine.
HABITAT/S Seasonally dry upland woodlands.

Helioceratops brachygnathus

— 1.3 m (4.3 ft) TL, 20 kg (40 lb)
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Lower jaw very deep along entire length.
AGE Late Early Cretaceous or early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Northeastern China; Quantou.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.

Zhuchengceratops inexpectus

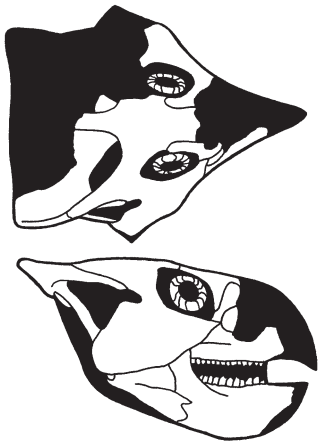
— 2.5 m (8 ft) TL, 175 kg (380 lb)
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Lower jaw extremely deep and massive.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Xingezhuang.

Yamaceratops dorngobiensis

— 0.5 m (1.7 ft) TL, 2 kg (4 lb)
FOSSIL REMAINS Majority of skull and minority of skeletons.
ANATOMICAL CHARACTERISTICS Frill short, fairly broad.
AGE Probably Late Cretaceous, possibly Santonian or Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; Javkhlant.

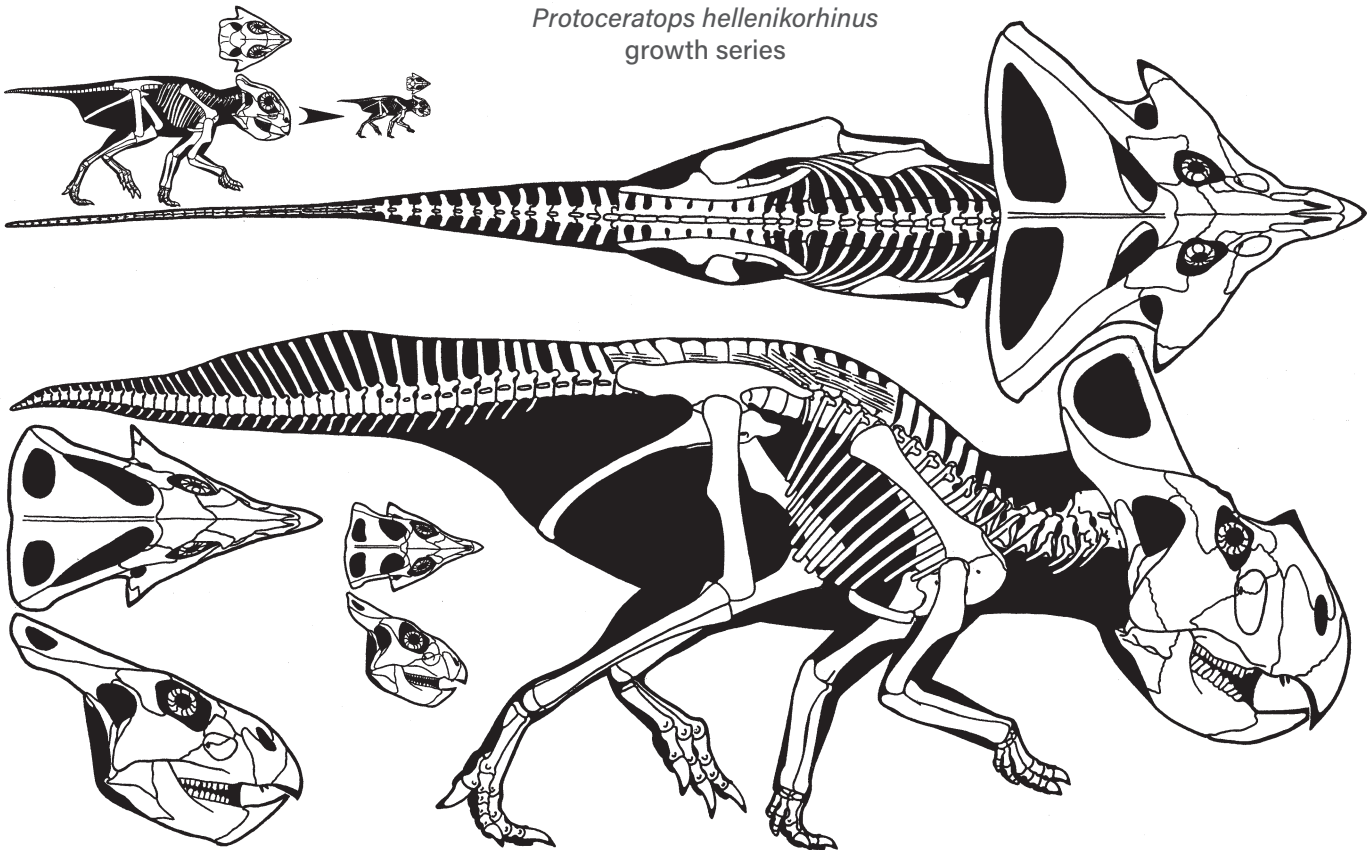
Protoceratops andrewsi

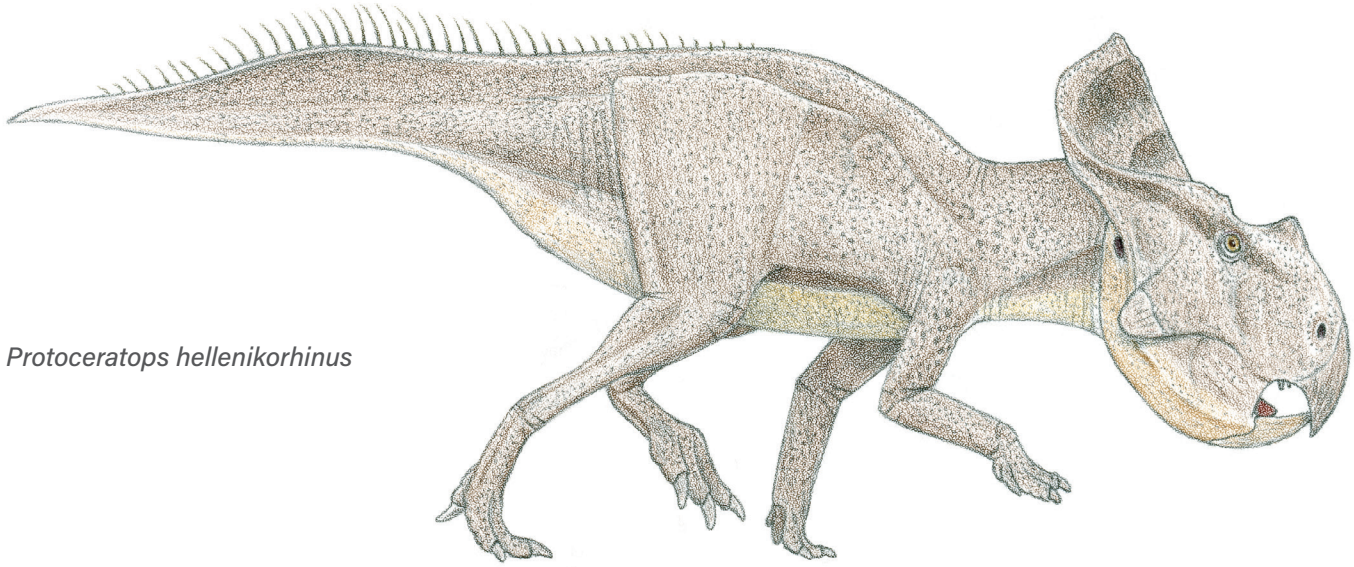
— 2.5 m (8 ft) TL, 190 kg (425 lb)
FOSSIL REMAINS Many dozens of skulls and skeletons, many complete, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Head very large and broad, deep, incipient nasal horn, frill large and broad, two teeth under upper beak. Tall vertebral spines over tail form a shallow sail.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Mongolia, northern China; lower Djadokhta, Minhe.
HABITAT/S Desert with dunes and oases.



Yamaceratops dorngobiensis

Protoceratops hellenikorhinus
growth series





Protoceratops hellenikorhinus

HABITS Large numbers of nestlings in nests indicate poorly ossified juveniles remained in nests for a period under parental care.
NOTES The classic protoceratopsid. Most immature remains not well described. Famous fighting pair preserves a *Velociraptor* and *Protoceratops* locked in comortal combat. May be direct ancestor of *P. hellenikorhinus*.

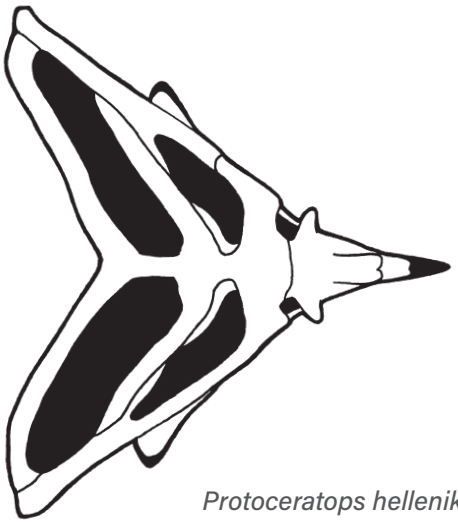
Protoceratops hellenikorhinus?

— 2.5 m (8 ft) TL, 190 kg (425 lb)
FOSSIL REMAINS Several skulls and minority of skeletons.
ANATOMICAL CHARACTERISTICS Head very large and broad, deep; nasal horn prominent; frill large and very broad, two teeth under upper beak.
AGE Late Cretaceous, late Campanian.

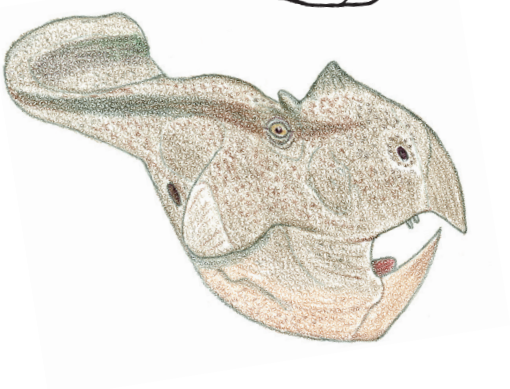
DISTRIBUTION AND FORMATION/S Mongolia; Wulansuhai, upper Djadokhta?
HABITAT/S Desert with dunes and oases.

Breviceratops kozlowskii

— Adult size uncertain
FOSSIL REMAINS Majority of skull and minority of skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Two teeth under upper beak.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.



Protoceratops hellenikorhinus?

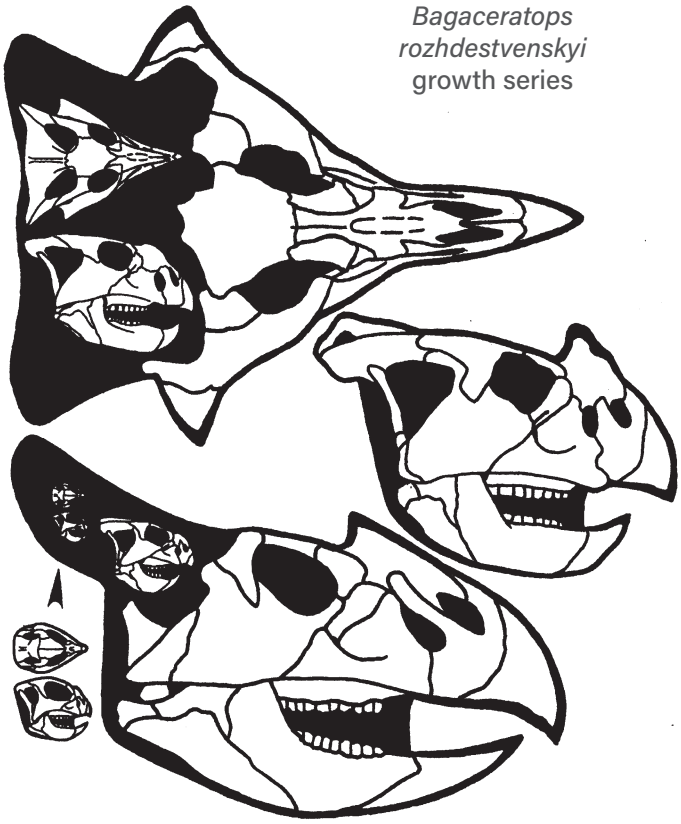


Bagaceratops rozhdestvenskyi

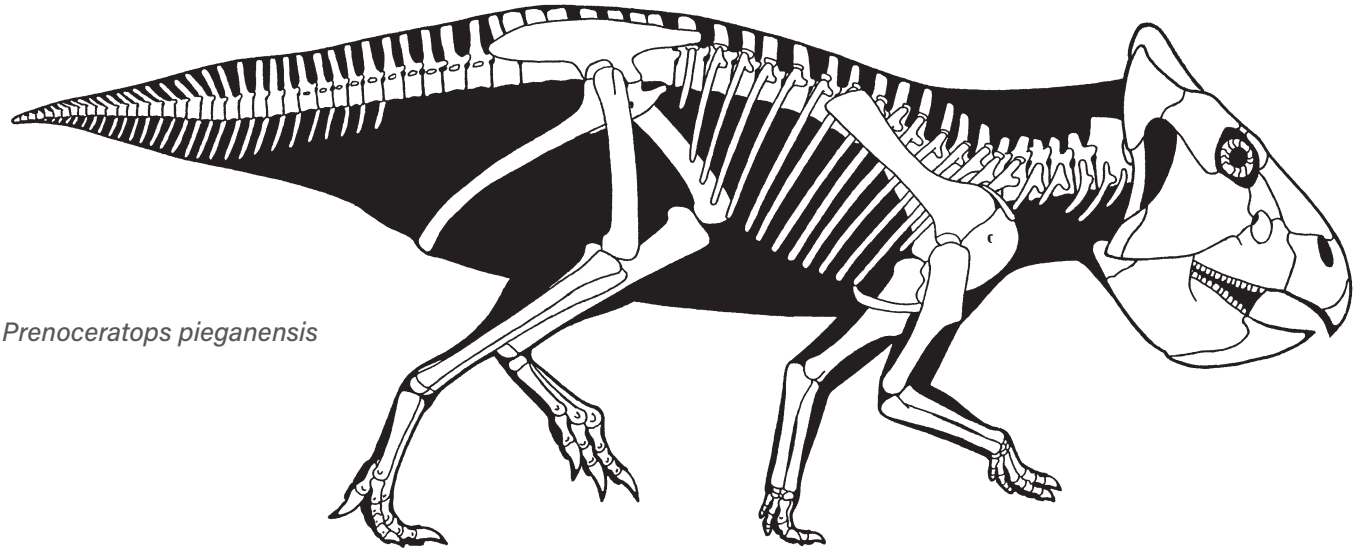
— 2.5 m (8 ft) TL, 200 kg (400 lb)
FOSSIL REMAINS Several complete skulls, numerous partial skulls and skeletons, adult and juvenile.
ANATOMICAL CHARACTERISTICS Head deep, nasal boss present, frill very short but broad, no teeth under upper beak.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Barun Goyot.
HABITAT/S Semidesert with some dunes and oases.
NOTES *Gobiceratops minutus*, *Lamaceratops tereschenkoi*, *Platyceratops tatarinovi*, and *Magnirostris dodsoni* probably juveniles of this species.

Udanoceratops tschizhovi

— 4 m (13 ft) TL, 750 kg (1,500 lb)
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head deep, nasal opening large, lower jaw extremely deep and massive, no teeth under upper beak. Arm short compared to hind limb, so possibly more bipedal than other protoceratopsids.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Mongolia; upper Djadokhta.



Bagaceratops rozhdestvenskyi growth series



Prenoceratops pieganensis

HABITAT/S Desert with dunes and oases.
HABITS Healed break in lower jaws implies intense impact combat within species.
NOTES May include *Bainoceratops efremovi*.

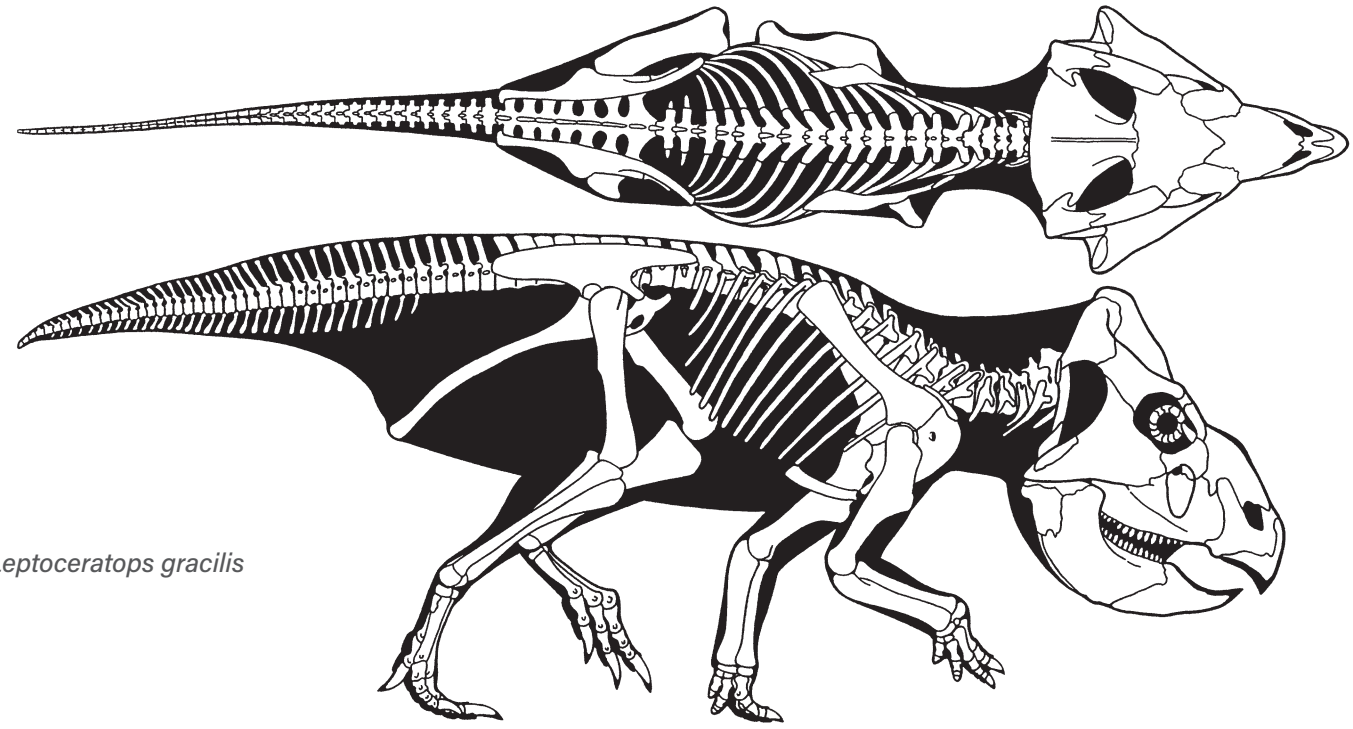
Prenoceratops pieganensis

— 1.3 m (4.3 ft) TL, 26 kg (55 lb)
FOSSIL REMAINS Complete skull and skeleton from large number of bones.
ANATOMICAL CHARACTERISTICS Head deep, full extent of frill uncertain, no teeth under upper beak, lower jaw very deep.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.
HABITAT/S Seasonally dry upland woodlands.

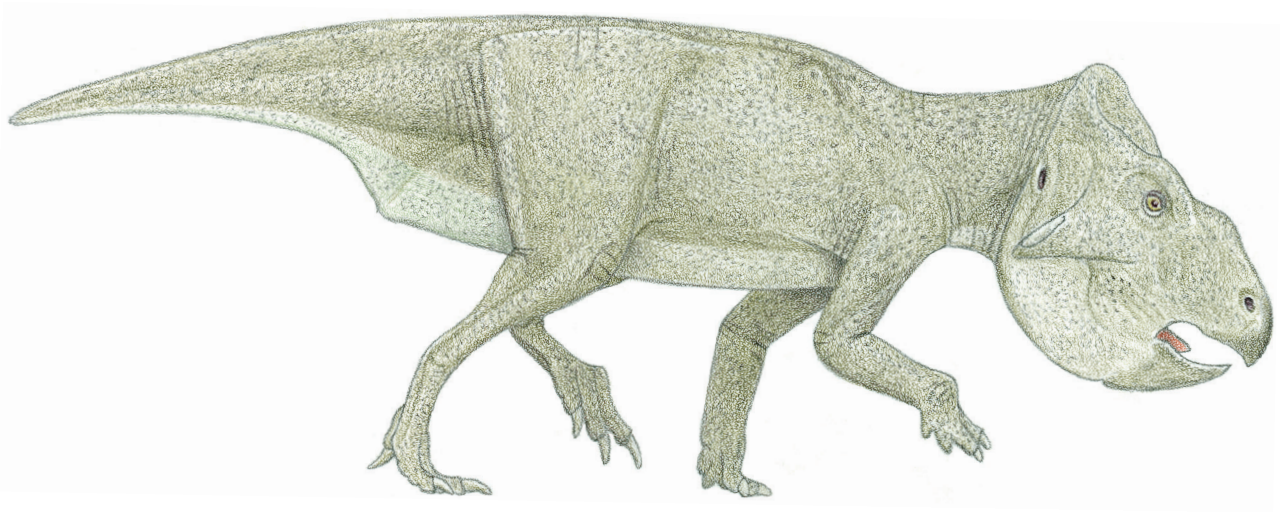
Leptoceratops gracilis

— 2 m (6.5 ft) TL, 100 kg (200 lb)
FOSSIL REMAINS Some skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head extremely large, deep, eyes shaded by overhanging rim, frill incipient, no teeth under upper beak, lower jaw very deep.
AGE Late Cretaceous, late Maastrichtian.

Leptoceratops gracilis



Leptoceratops gracilis



DISTRIBUTION AND FORMATION/S Montana, Wyoming, Alberta; Hell Creek, Lance, Scollard, levels uncertain.
HABITAT/S Upland forests.
NOTES May be more than one stratigraphic species.

Montanoceratops cerorhynchus

— 2.5 m (8 ft) TL, 190 kg (420 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Head deep, nasal horn absent, full extent of frill uncertain, no teeth under upper beak. Tall vertebral spines over tail form a shallow sail.
AGE Late Cretaceous, latest Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta, Montana; Saint Mary River, lower Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.

— CERATOPSOIDS

MEDIUM-SIZED TO GIGANTIC NEOCERATOPSIANS LIMITED TO THE LATE CRETACEOUS OF NORTH AMERICA AND ASIA.

ANATOMICAL CHARACTERISTICS Nasal openings enlarged, large nasal and/or brow horns usually present, coronoid processes on lower jaws well developed, no teeth under upper beaks.

— ZUNICERATOPSIDS

MEDIUM-SIZED CERATOPSOIDS LIMITED TO THE EARLY LATE CRETACEOUS OF NORTH AMERICA AND ASIA.

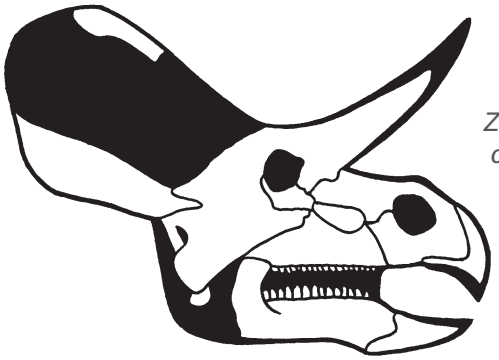
ANATOMICAL CHARACTERISTICS Brow horns well developed, no teeth under upper beaks, otherwise generally lacking features of ceratopsids.

Zuniceratops christopheri

— 2.2 m (6.5 ft) TL, 190 kg (400 lb)
FOSSIL REMAINS Several partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head long, no nasal horn, brow horns large, frill long.
AGE Late Cretaceous, middle Turonian.
DISTRIBUTION AND FORMATION/S New Mexico; Moreno Hill.
HABITAT/S Coastal swamps and marshes.
HABITS Horns and frills used as display organs and weapons during contests within species as well as for defense against theropods.

Turanoceratops tardabilis

— 2 m (6.5 ft) TL, 175 kg (390 lb)
FOSSIL REMAINS Minority of a few skulls and skeletons.
ANATOMICAL CHARACTERISTICS Brow horns large.
AGE Late Cretaceous, middle or late Turonian.
DISTRIBUTION AND FORMATION/S Uzbekistan; Bissekty.
HABITAT/S Coastal.

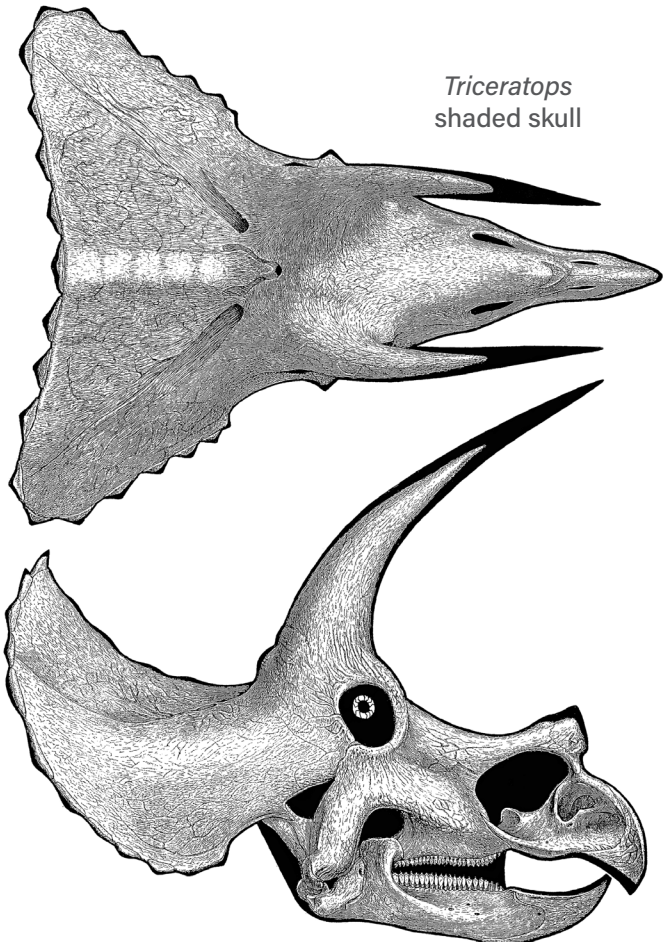


Zuniceratops christopheri

— CERATOPSIDS

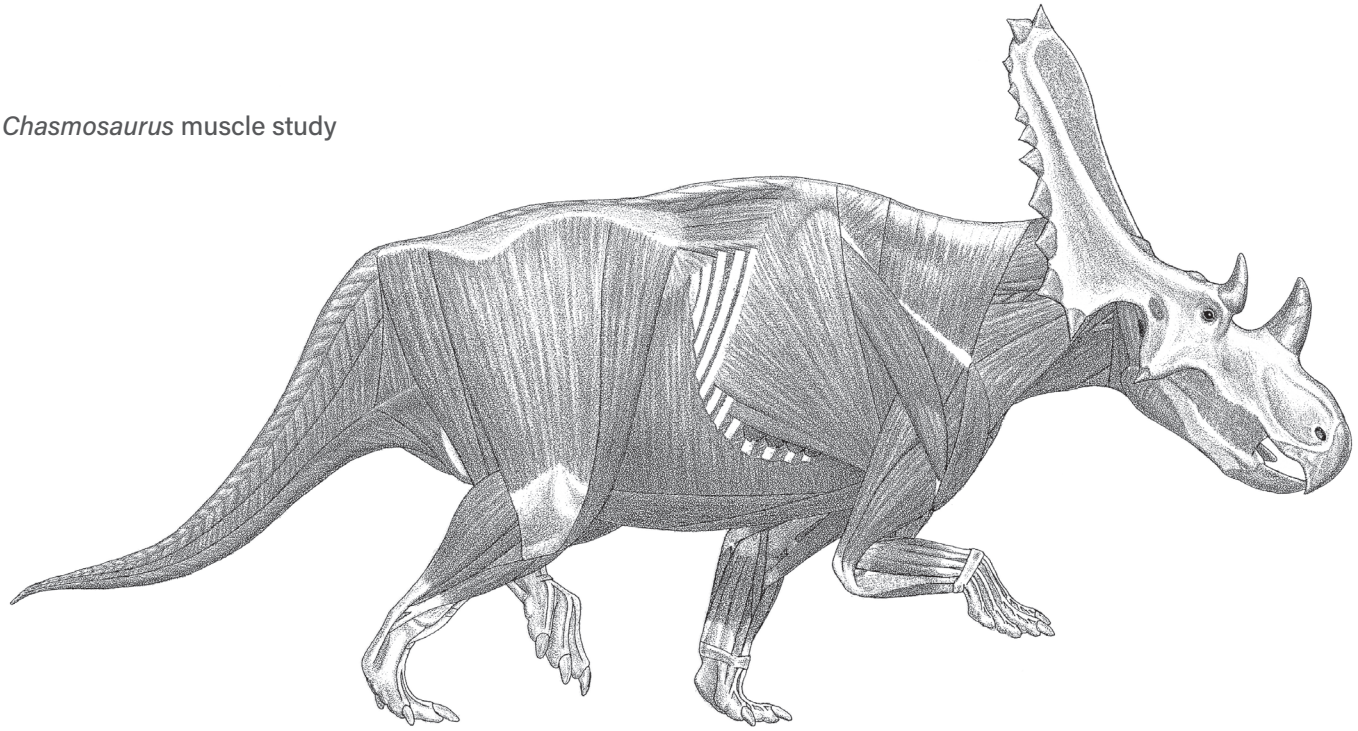
LARGE TO GIGANTIC CERATOPSOIDS LIMITED TO THE LATE LATE CRETACEOUS OF NORTH AMERICA AND ASIA.

ANATOMICAL CHARACTERISTICS Fairly uniform except for head adornments. Upper beaks hooked, lack teeth, nasal openings very large, assorted bosses and hornlets on skulls, head frills often well developed, main tooth rows long and developed into complex subvertical slicing batteries containing hundreds of teeth. Skeletons heavily constructed. First neck vertebrae fused together. Ribs in front of hips contact one another and anterior pubic processes of pelves. Tails sweep downward, shortened. Trackways indicate hands farther from midline than hind feet. Fingers shorter. Pelves very large, indicating exceptional muscle power, toes shorter.
ONTOGENY Growth rates apparently rapid, probably to reduce exposure to and recover from predation.
HABITS Some species may have fed in shallow waters on occasion; may have scavenged carcasses. Horns and frills used as display organs and weapons during contests within species; rib cage cuirass may have helped protect flanks. Defense may have included rearing like a bear and tilting frill up to intimidate attacker, followed by short fast charge with horns and/or beaks. Frills and in some cases spikes helped protect neck. Single-species bone beds indicate at least some species sometimes congregated in large herds.
NOTES Closest mammal analogues rhinos and giant extinct suids.



Triceratops shaded skull

Chasmosaurus muscle study



— CENTROSAURINES

LARGE CERATOPSIDS LIMITED TO THE LATE LATE CRETACEOUS OF NORTH AMERICA AND ASIA.

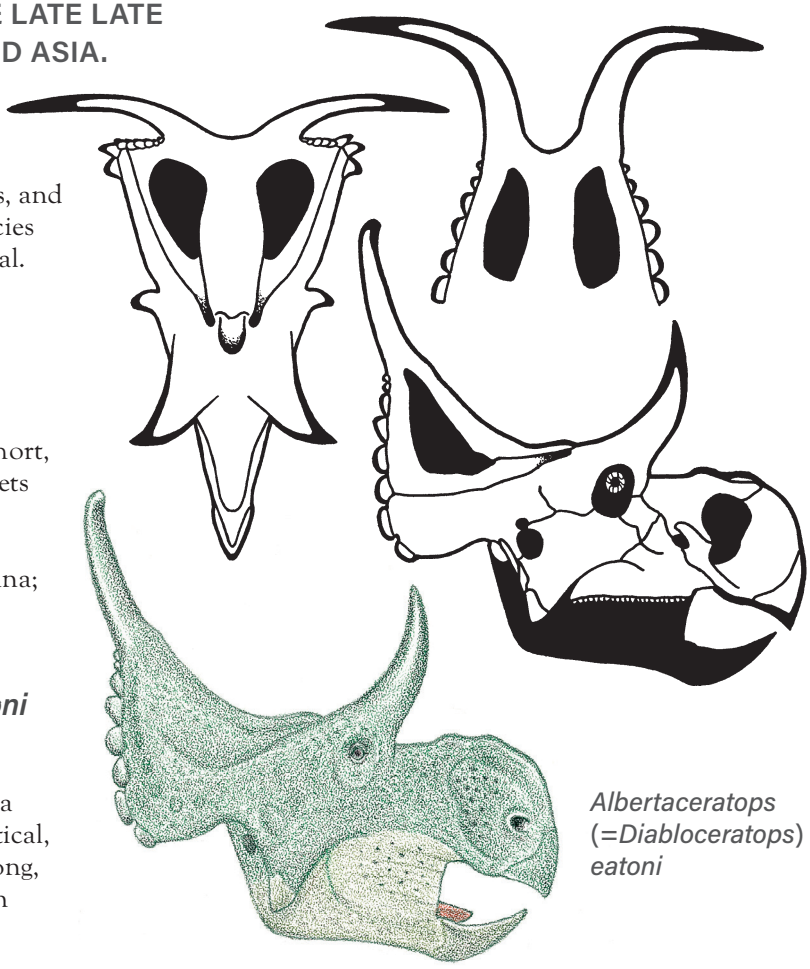
ANATOMICAL CHARACTERISTICS Fairly uniform except for head adornments. Nasal openings subcircular, frills not always strongly elongated, open and subcircular; horns, hornlets, and bosses often exceptionally variable within a species and frequently asymmetrical within an individual. Pelvic ilia slope downward and backward.

Sinoceratops zhuchengensis

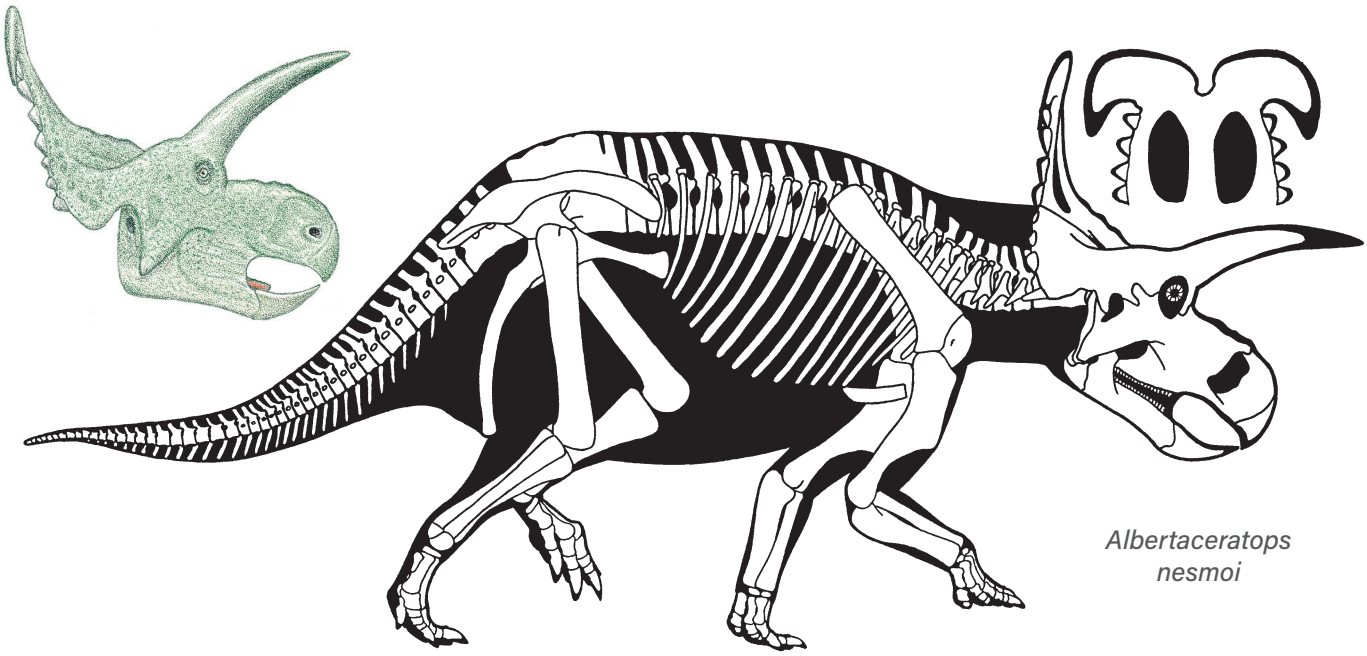
— 5 m (17 ft) TL, 2.5 tonnes
FOSSIL REMAINS Two partial skulls.
ANATOMICAL CHARACTERISTICS Nasal horn short, brow horns absent, large, upward-curving hornlets on back rim of frill.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Xingezhuang.
NOTES Only known ceratopsid from Asia.

Albertaceratops (= *Diabloceratops*) *eatoni*

— 4.5 m (14 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Nasal boss is a low, narrow ridge, brow horns large, frill subvertical, tilted strongly upward, back rim with a pair of long, outward-arcing, slender spikes, small hornlets on rim side.
AGE Late Cretaceous, early Campanian.



Albertaceratops (=*Diabloceratops*) *eatoni*



Albertaceratops nesmoi

DISTRIBUTION AND FORMATION/S Utah; upper Wahweap.
NOTES Appears to be within *Albertaceratops*.

Albertaceratops nesmoi

— 5.8 m (19 ft) TL, 4.2 tonnes
FOSSIL REMAINS Majority of a skull, and majority of skeleton from bone beds.
ANATOMICAL CHARACTERISTICS Nasal boss is a low, narrow ridge, brow horns fairly large, frill subvertical, back rim with a pair of massive, side and forward-arcing hornlets, small hornlets on rim side.
AGE Late Cretaceous, early middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Oldman.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Albertaceratops (= *Medusaceratops*) *lokii*

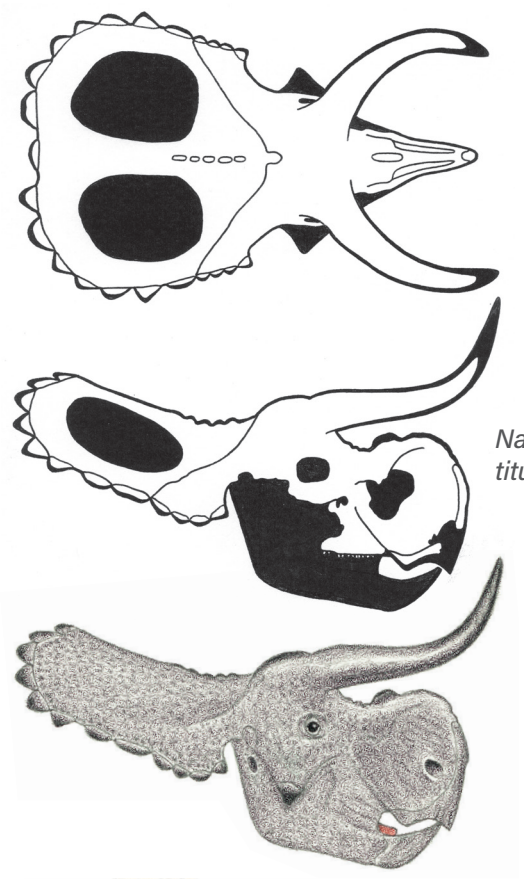
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Bone bed remains, possible partial juvenile skull and skeleton.
ANATOMICAL CHARACTERISTICS Nasal boss is a low, narrow ridge, brow horns large, back rim of frill with a pair of massive, side and forward-arcing hornlets, next side hornlet similar but smaller, rest of side hornlets small.
AGE Late Cretaceous, early middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; lower Judith River.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.
NOTES Incomplete and inadequate, lacks skull top, contemporary *Avaceratops lammersi* may be juvenile of this species or genus, in which case there are issues concering the generic titles of albertaceratopsians; this species appears to be within *Albertaceratops*. Placement of a larger immature skull fossil from higher in formation in this taxon not correct.

Furcatoceratops (or *Nasutoceratops*) *elucidans*

— Adult size uncertain
FOSSIL REMAINS Majority of skull and skeleton, immature.
ANATOMICAL CHARACTERISTICS Nasal horn/boss barely present, medium-sized brow horns curved strongly forward.
AGE Late Cretaceous, early late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Judith River.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.
HABITS Forward-directed brow horns indicate frontal thrusting action.
NOTES A somewhat larger immature skull from same level of formation that has incorrectly been placed in much earlier *Avaceratops* does not appear to be same as this species, the skull of which lacks much of snout and frill; may be a species of *Nasutoceratops*.

Nasutoceratops titusi

— 4.5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Majority of skulls and minority of a skeleton.
ANATOMICAL CHARACTERISTICS Nasal horn/boss barely present, large bovid-like brow horns subhorizontal, tips point a little inward, frill subhorizontal, subcircular, all hornlets small.



Nasutoceratops titusi

AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Utah; middle Kaiparowitz.
HABITS Forward-directed brow horns indicate frontal thrusting action.

Wendiceratops pinhornensis

— 4.5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS Numerous skull and skeletal elements and majority of skeleton from bone beds.
ANATOMICAL CHARACTERISTICS Nasal horn well developed, brow horns large, subvertical, frill subhorizontal, back rim subcircular, back rim with large, broad, forward-directed hornlets.
AGE Late Cretaceous, early middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Oldman.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Centrosaurus (= *Coronosaurus*) *brinkmani*

— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Bone bed remains.
ANATOMICAL CHARACTERISTICS Nasal horn moderately large and erect, brow horns small and directed sideways, frill subhorizontal, large hornlets project from back rim over openings with bases sprouting minihornlets, innermost rim edge hornlets large and projecting sideways, small hornlets adorn sides of rim.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park, upper Oldman.
HABITS Vertically directed nasal horn indicates upward thrusting action.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be direct ancestor of *C. apertus*.

Centrosaurus apertus

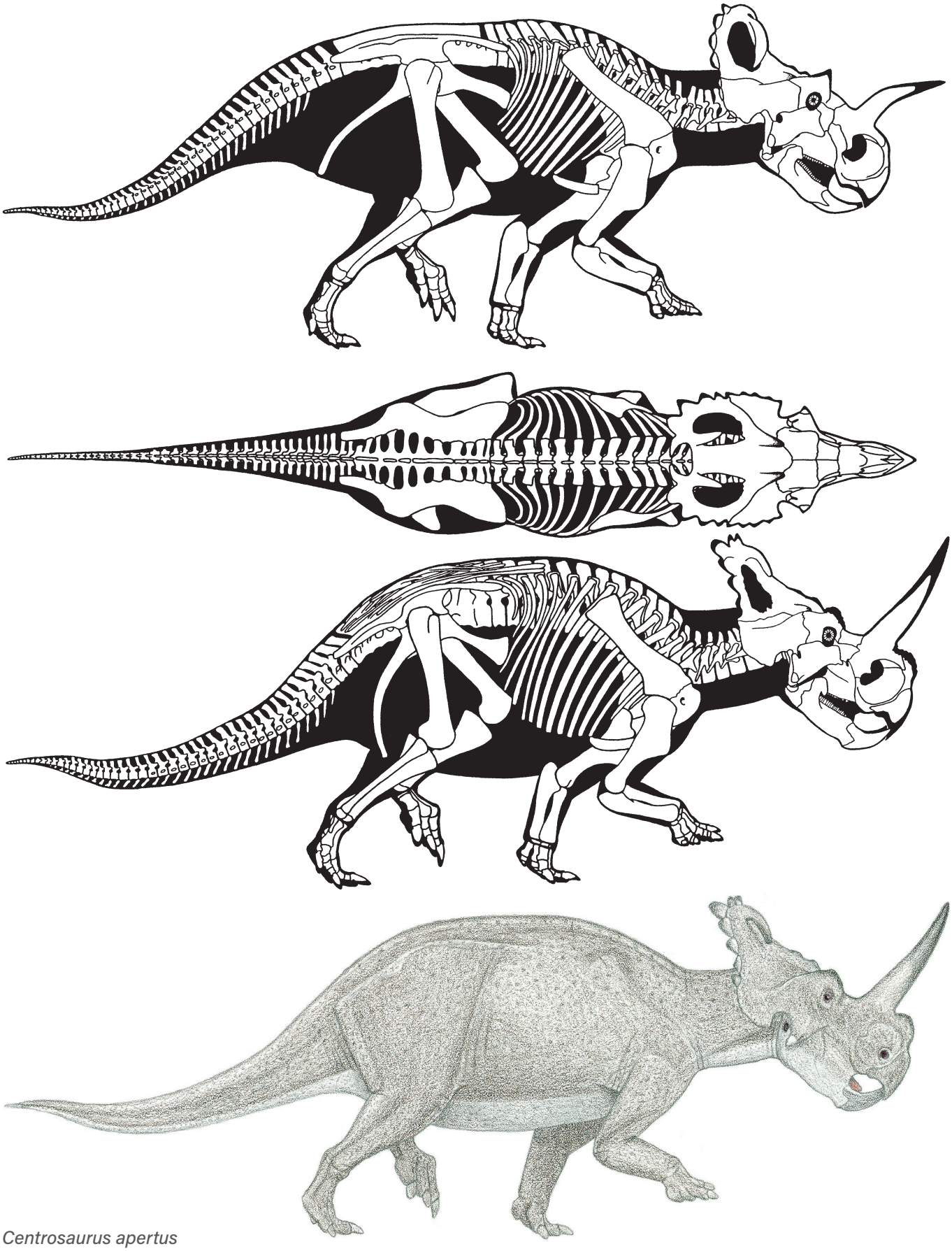
— 5.5 m (18 ft) TL, 2.3 tonnes
FOSSIL REMAINS A number of complete and partial skulls and skeletons, bone beds, skin impressions, completely known.
ANATOMICAL CHARACTERISTICS Large nasal horn curved from strongly forward to a little backward, brow horns small, frill subhorizontal, subhorns project from back rim over openings, sometimes strongly asymmetrical in length, innermost rim edge hornlets point toward centerline, small hornlets adorn sides of rim.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Probably includes *C. nasicornis* and *C. cutleri*. May be the direct descendant of *C. brinkmani*. Remains from the Judith River Formation of Montana named *Monoclonius* are based on inadequate remains and probably belong to this genus.

Centrosaurus (= *Spinops*) *sternbergorum*

— 4.5 m (14 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skulls.
ANATOMICAL CHARACTERISTICS Nasal horn large, brow horns small, subhorns project from back rim over openings, a large spike projects straight back from both sides of rim edge, small hornlets adorn sides of rim.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; uppermost Oldman or lower Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be an ancestor of *C. albertensis*.

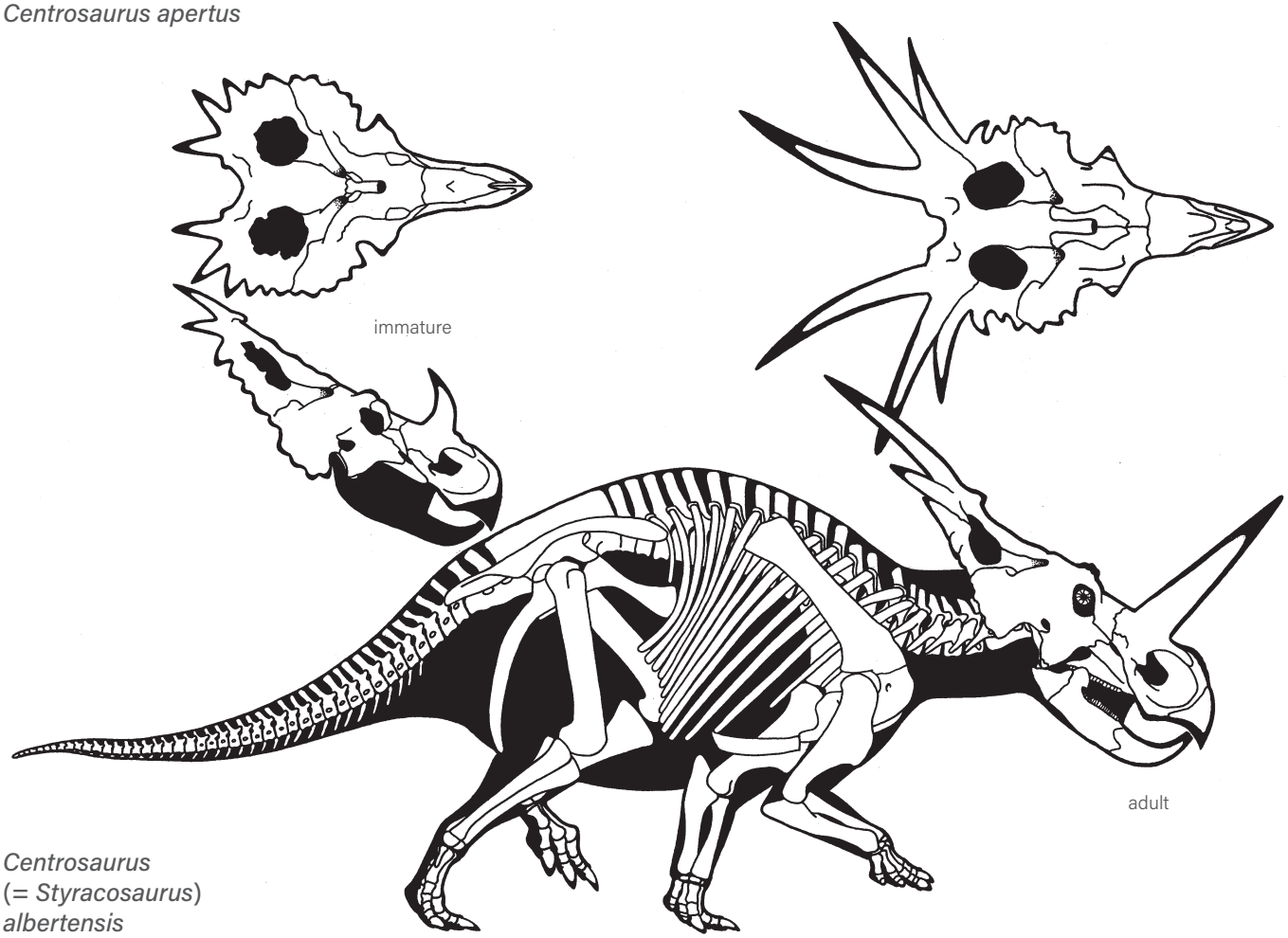
Centrosaurus (= *Styracosaurus*) *albertensis*

— 5.1 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS A few complete and partial skulls and skeletons, bone bed remains.
ANATOMICAL CHARACTERISTICS Large nasal horn, brow horns small, frill subhorizontal, rimmed by array of large spikes, innermost projecting sideways, small hornlets on rim side.
AGE Late Cretaceous, middle late Campanian.

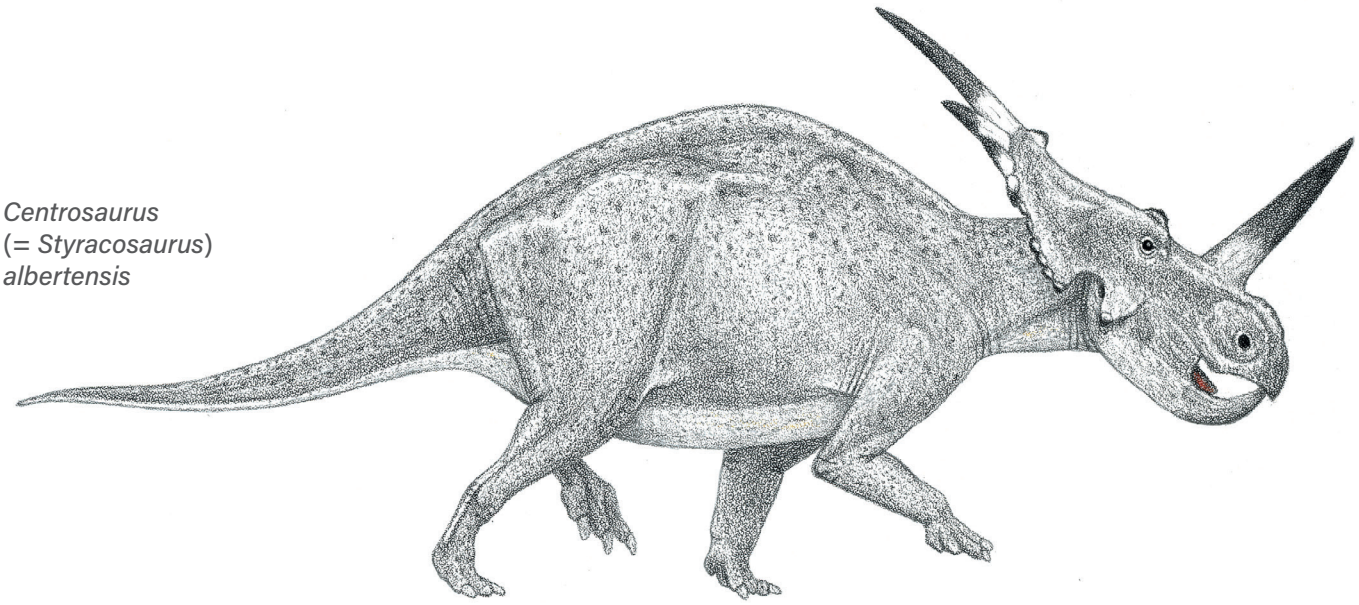


Centrosaurus apertus

Centrosaurus apertus



Centrosaurus
(= *Styracosaurus*)
albertensis



Centrosaurus (= *Styracosaurus*) *albertensis*

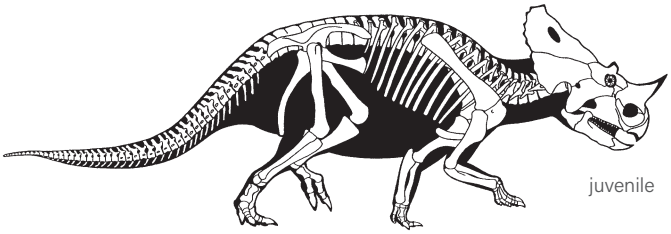
DISTRIBUTION AND FORMATION/S Alberta; upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Vertically directed nasal horn indicates upward thrusting action.
NOTES Because the skulls and skeletons of centrosaurines without large brow horns and subhorizontal frills are very similar except for the details of the horns, bosses, and frills, they probably form one genus.

Centrosaurus (= *Rubeosaurus*) *ovatus*

— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Numerous skull and skeletal remains, possibly including juveniles.
ANATOMICAL CHARACTERISTICS Large nasal horn, brow horns small, frill subhorizontal, rimmed by array of large spikes, innermost spikes converge inward.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.
HABITS Vertically directed nasal horn indicates upward thrusting action.
HABITAT/S Seasonally dry upland woodlands.
NOTES May be splittable into additional species, *C.* (*Stellasaurus*) *ancellae*. Fossils may include juveniles.

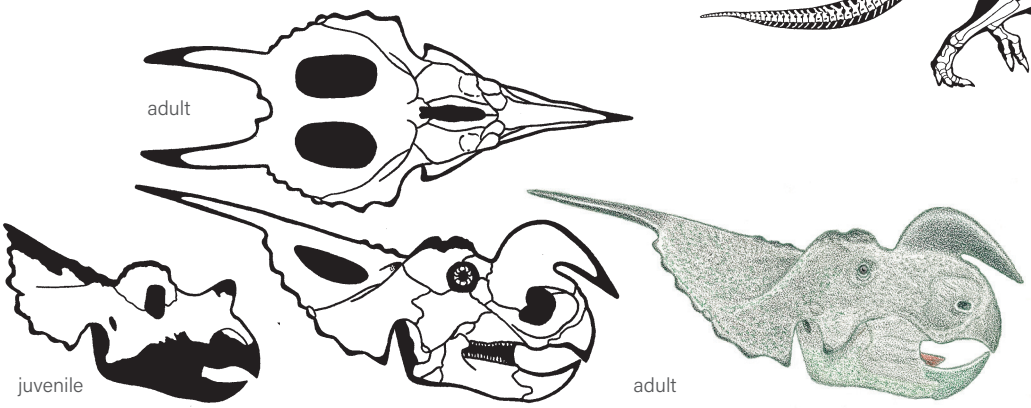
Centrosaurus (= *Einiosaurus*) *procurvicornis*

— Adult size uncertain
FOSSIL REMAINS Several partial skulls and a number of skeletons, juvenile to near adult.
ANATOMICAL CHARACTERISTICS Large nasal horn strongly downcurved and deep; brow horns small, frill subhorizontal, two long spikes near middle of back rim, small hornlets on rim side.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.
HABITAT/S Seasonally dry upland woodlands.



juvenile

Centrosaurus (= *Rubeosaurus*) *ovatus*



adult

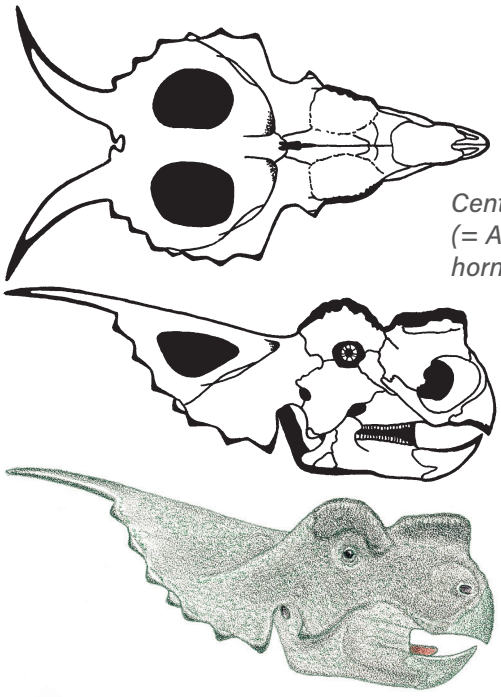
juvenile

adult

Centrosaurus (= *Einiosaurus*) *procurvicornis*

HABITS May have rammed other members of species and tyrannosaurids with edge of horn; primary weapon against latter was its beak.
NOTES Taxonomically inadequate juvenile remains named *Brachyceratops montanensis* may belong to this species, alternatively to *C. ovatus*.

Centrosaurus (= *Achelousaurus*) *horneri*
— 6 m (20 ft) TL, 3 tonnes
FOSSIL REMAINS Several partial skulls and a partial skeleton.
ANATOMICAL CHARACTERISTICS Nasal and brow bosses present, frill subhorizontal, two long, partly sideways-arcing spikes near middle of back rim, small hornlets on rim side.

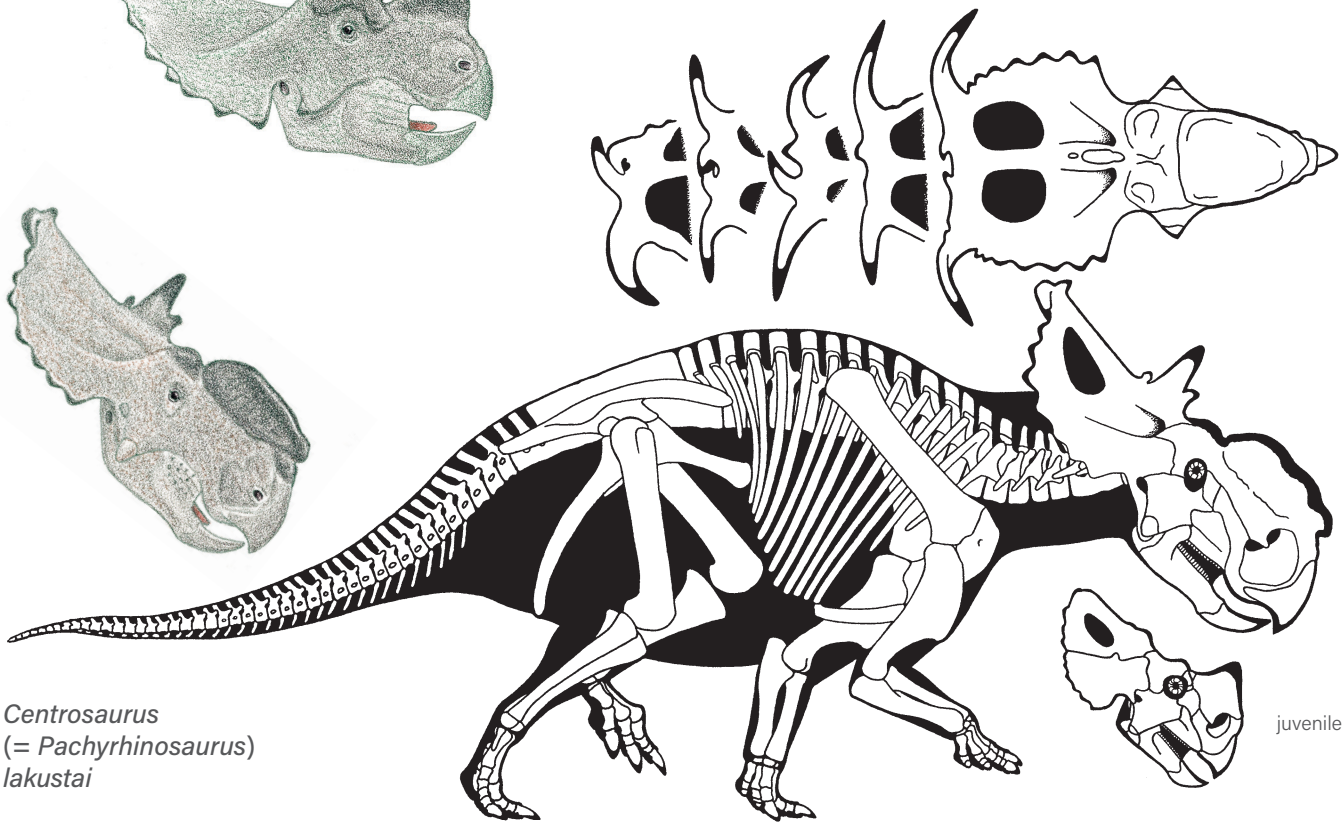


Centrosaurus (= Achelousaurus) horneri

AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana; upper Two Medicine.

Centrosaurus (= *Pachyrhinosaurus*) *lakustai*
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS A very large number of partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Nasal and brow bosses replace low juvenile nasal horn and combine into a massive unit in adults, frill subhorizontal, center strut bears irregular short vertical horn/nub/hump(s) in at least one adult morph, two sideways-sweeping spikes on back rim, two small horns along midline point toward each other, small hornlets on rim side.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; middle Wapiti.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, winters cool to cold.
NOTES Presence of keratin horns atop bosses cannot be entirely ruled out in pachyrhinosaurs. May be direct ancestor of *C. canadensis*.

Centrosaurus (= *Pachyrhinosaurus*) *canadensis*
— 6 m (20 ft) TL, 3 tonnes
FOSSIL REMAINS A large number of partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Nasal and brow bosses present in juveniles, combine into a massive unit in adults,

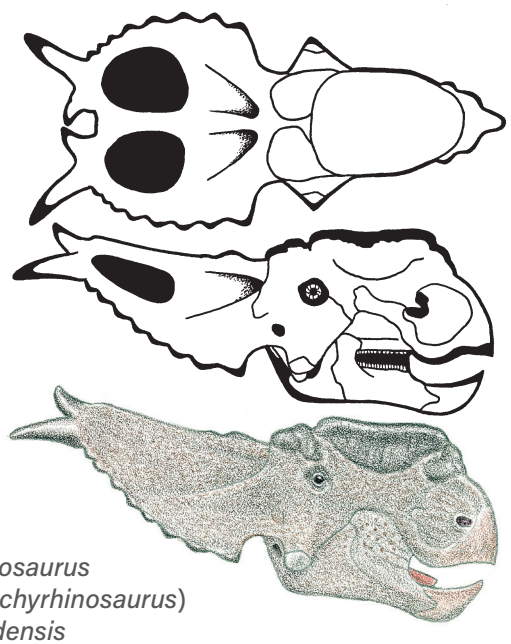


Centrosaurus (= Pachyrhinosaurus) lakustai

juvenile

frill subhorizontal, two backward- and sideways-pointing spikes on back rim, two small horns along midline point toward each other, small hornlets on rim side.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower Horseshoe Canyon, Saint Mary River.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, winters cool to cold.

Centrosaurus (= Pachyrhinosaurus) perotorum
— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skulls.
ANATOMICAL CHARACTERISTICS Spikes on frill rim robust, small frill hornlets project forward.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern Alaska; middle Prince Creek.
HABITAT/S Well-watered coastal woodland, cool summers, severe winters including heavy snows.
NOTES Indicates that polar ceratopsids were not dwarfed compared to those from farther south.



Centrosaurus (= *Pachyrhinosaurus*) *canadensis*

— CHASMOSAURINES

LARGE TO GIGANTIC CERATOPSIDS LIMITED TO THE LATE LATE CRETACEOUS OF NORTH AMERICA.

ANATOMICAL CHARACTERISTICS Nasal openings elongated, frills always long and open. Tails generally shorter than those of centrosaurines. Pelvic ilia horizontal.
HABITS Short-horned species and individuals relied more on beaks than horns for defense.

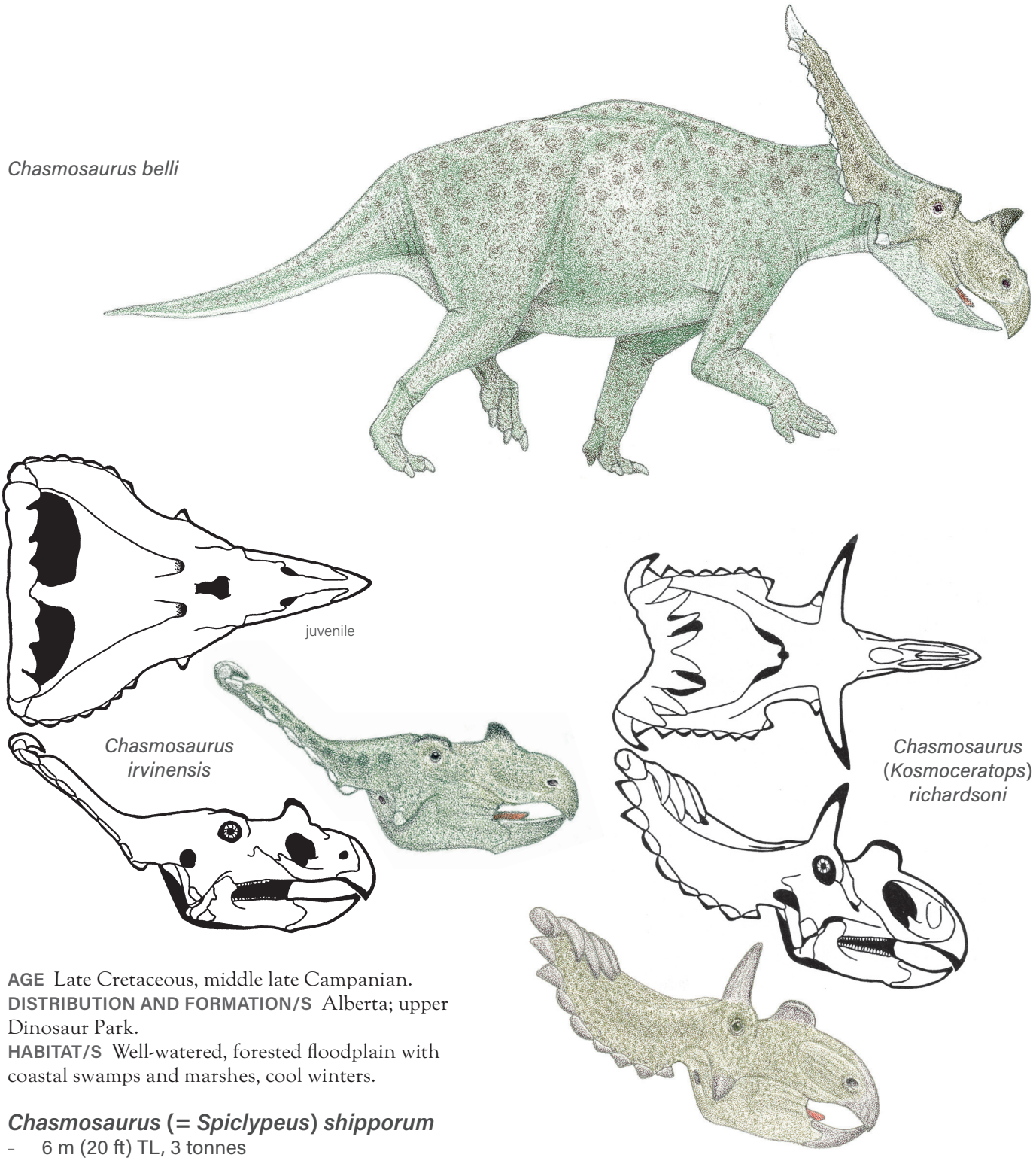
Coahuilaceratops magnacuerna
— 4 m (13 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Nasal horn low, brow horns very large.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Northern Mexico; middle Cerro del Pueblo.

Chasmosaurus russelli (see p.318)
— 4.3 m (14 ft) TL, 1.7 tonnes
FOSSIL REMAINS Several complete or partial skulls, partial skeleton.
ANATOMICAL CHARACTERISTICS Nasal horn short, brow horns short or long, frill subhorizontal, back rim very broad and forming a U, corners with large hornlets, small hornlets along side rims. Shoulder withers supported nuchal ligaments to neck and head. Belly broad, hind legs bowed.
AGE Late Cretaceous, late middle to middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower to upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May include C. (*Mojoceratops*) *perifania*.

Chasmosaurus belli (see pp.318-319)
— 4.8 m (16 ft) TL, 2.3 tonnes
FOSSIL REMAINS A number of skulls and skeletons, completely known.
ANATOMICAL CHARACTERISTICS Nasal and brow horns short, orientation variable, frill subhorizontal, back rim very broad and nearly straight, corners with large hornlets, small hornlets along side rims. Shoulder withers supported nuchal ligaments to neck and head. Belly broad, hind legs bowed.
AGE Late Cretaceous, early late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; middle Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be the direct descendant of *C. russelli*.

Chasmosaurus irvinensis
— 4.5 m (15 ft) TL, 2 tonnes
FOSSIL REMAINS A few skulls and majority of distorted skeleton.
ANATOMICAL CHARACTERISTICS Nasal horn short, brow horns absent, frill not as elongated as in other *Chasmosaurus*, back rim very broad, straight, bearing a row of large, broad, forward-directed hornlets, small hornlets along side rims. Belly broad and hind legs bowed.

Chasmosaurus russelli
immature *C. belli* or *russelli*
juvenile
Chasmosaurus belli



AGE Late Cretaceous, middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

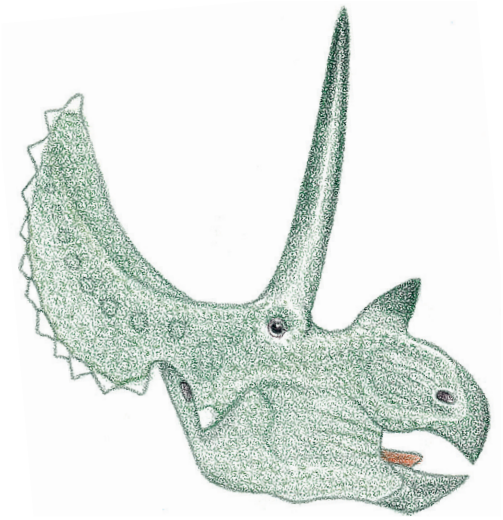
Chasmosaurus (= *Spiclypeus*) *shipporum*

– 6 m (20 ft) TL, 3 tonnes
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Nasal horn small, moderate-sized brow horns project strongly to sides, large subtriangular hornlets at back outer corners of frill, central hornlets united into forward-curling subrectangular flange.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; middle Judith River.

Chasmosaurus (*Kosmoceratops*) *richardsoni*

—— 4.5 m (15 ft) TL, 2 tonnes
FOSSIL REMAINS A complete skull and partial skulls.
ANATOMICAL CHARACTERISTICS Nasal horns short, long, blunt, brow horns large and projecting sideways, frill not as elongated as in other *Chasmosaurus*, back rim broad, somewhat indented, bearing a row of large,

broad, forward-directed hornlets, also forward- and sideways-projecting hornlets at rim corners, small hornlets along side rims.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Utah; lower to upper Kaiparowits.
NOTES With only frills greatly differing from *Chasmosaurus*, this and *C. irvinensis* probably within former genus; alternatively they form a united genus.



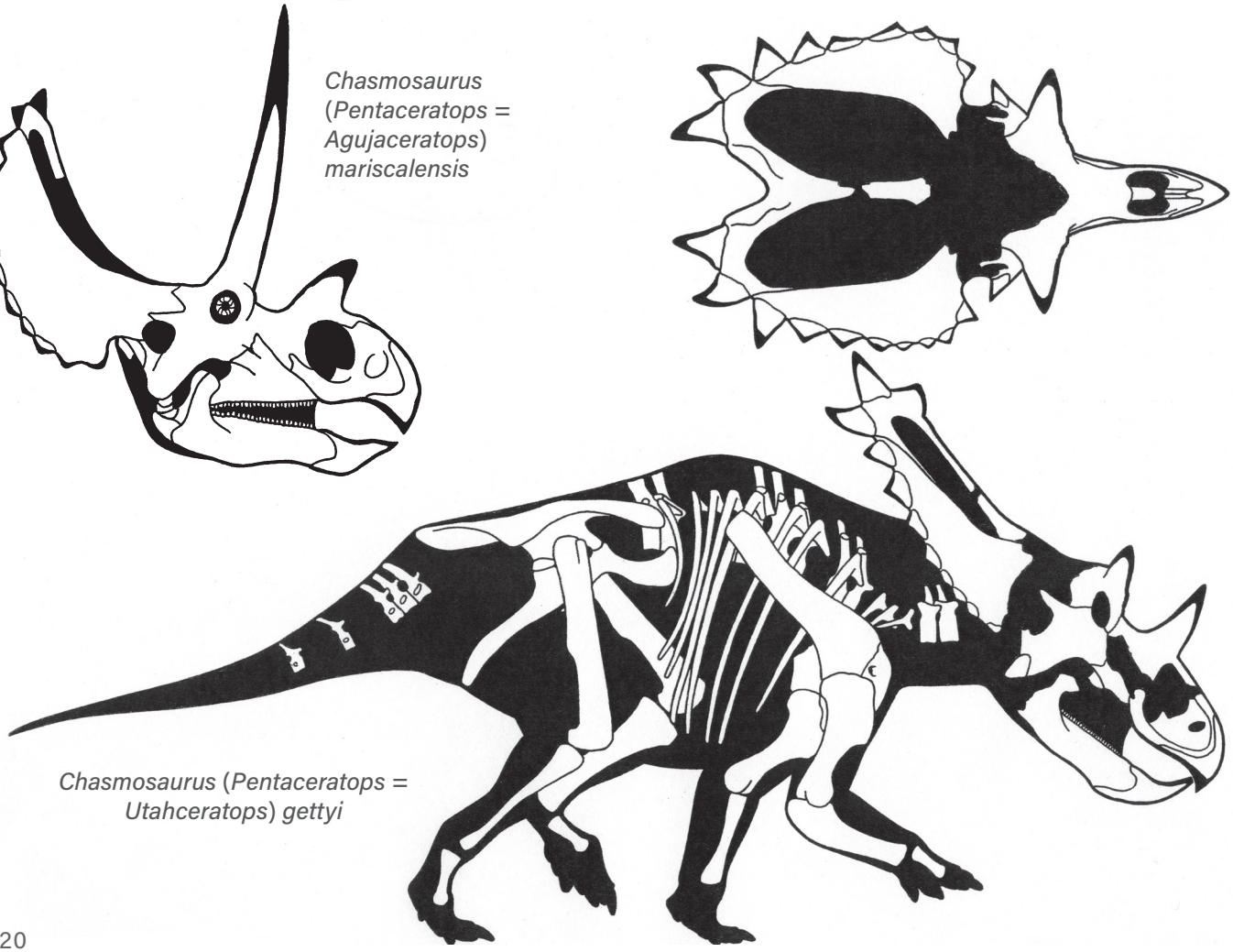
Chasmosaurus (*Pentaceratops* = *Agujaceratops*) *mariscalensis*

— 4.3 m (14 ft) TL, 1.5 tonnes
FOSSIL REMAINS Numerous disarticulated skulls and skeletons, juvenile to adult.
ANATOMICAL CHARACTERISTICS Nasal horn short, brow horns long, frill elongated, back rim not broad, strongly indented, bearing large hornlets, small hornlets along side rims. Belly broad, hind legs bowed.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Texas; Aguja.
NOTES Originally placed in *Chasmosaurus*; the skulls and skeletons of the chasmosaurs are very similar except for the horns and frills, so they probably form one genus. Alternatively, this, *Utahceratops gettyi*, and *Pentaceratops sternbergii* form a united genus.

Chasmosaurus (*Pentaceratops* = *Utahceratops*) *gettyi*

— 5 m (16 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Nasal and brow horns short, latter projecting sideways, frill elongated, back rim not broad, strongly indented, bearing large hornlets, innermost projecting vertically, small hornlets along side rims.

Chasmosaurus (*Pentaceratops* = *Agujaceratops*) *mariscalensis*

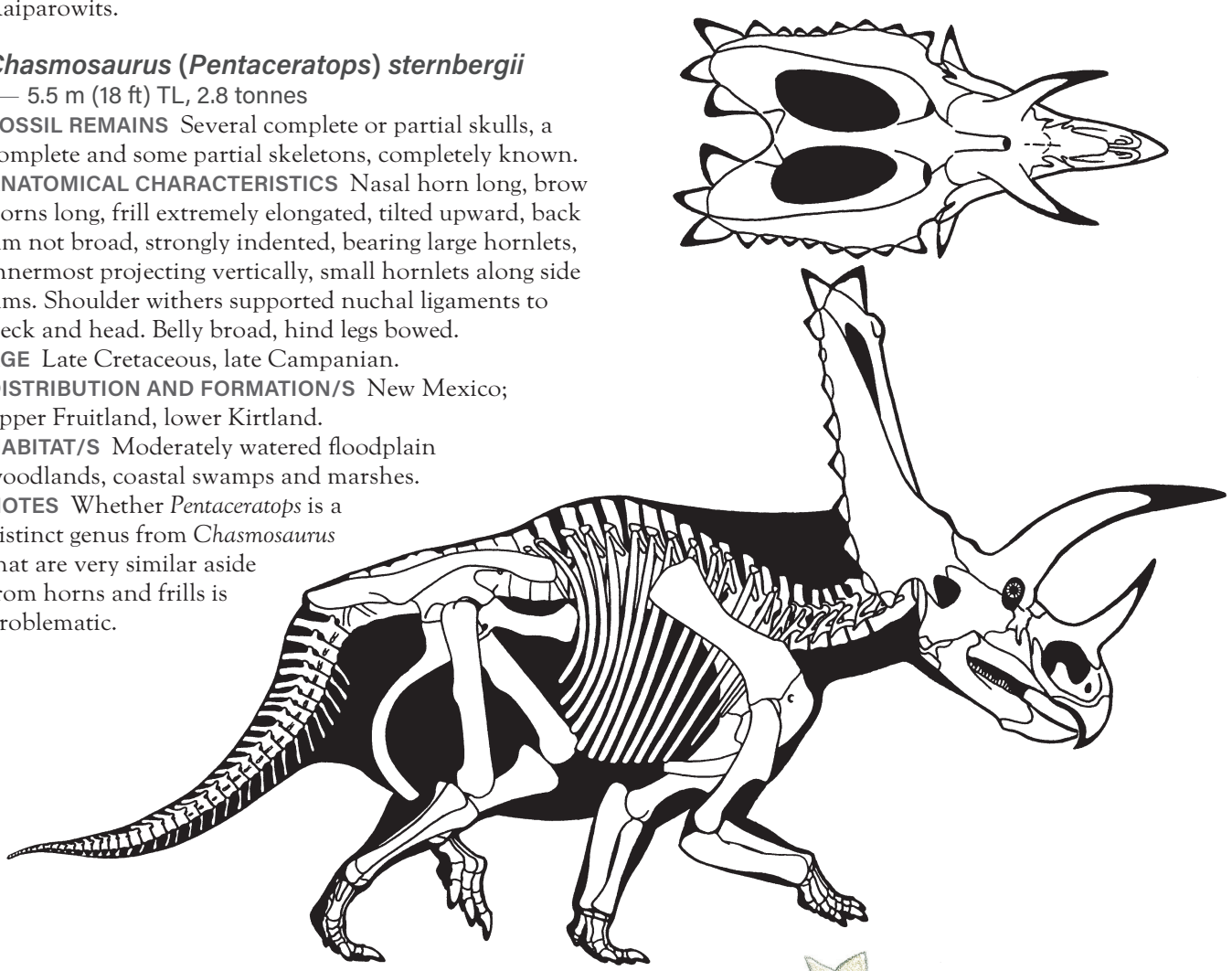


Chasmosaurus (*Pentaceratops* = *Utahceratops*) *gettyi*

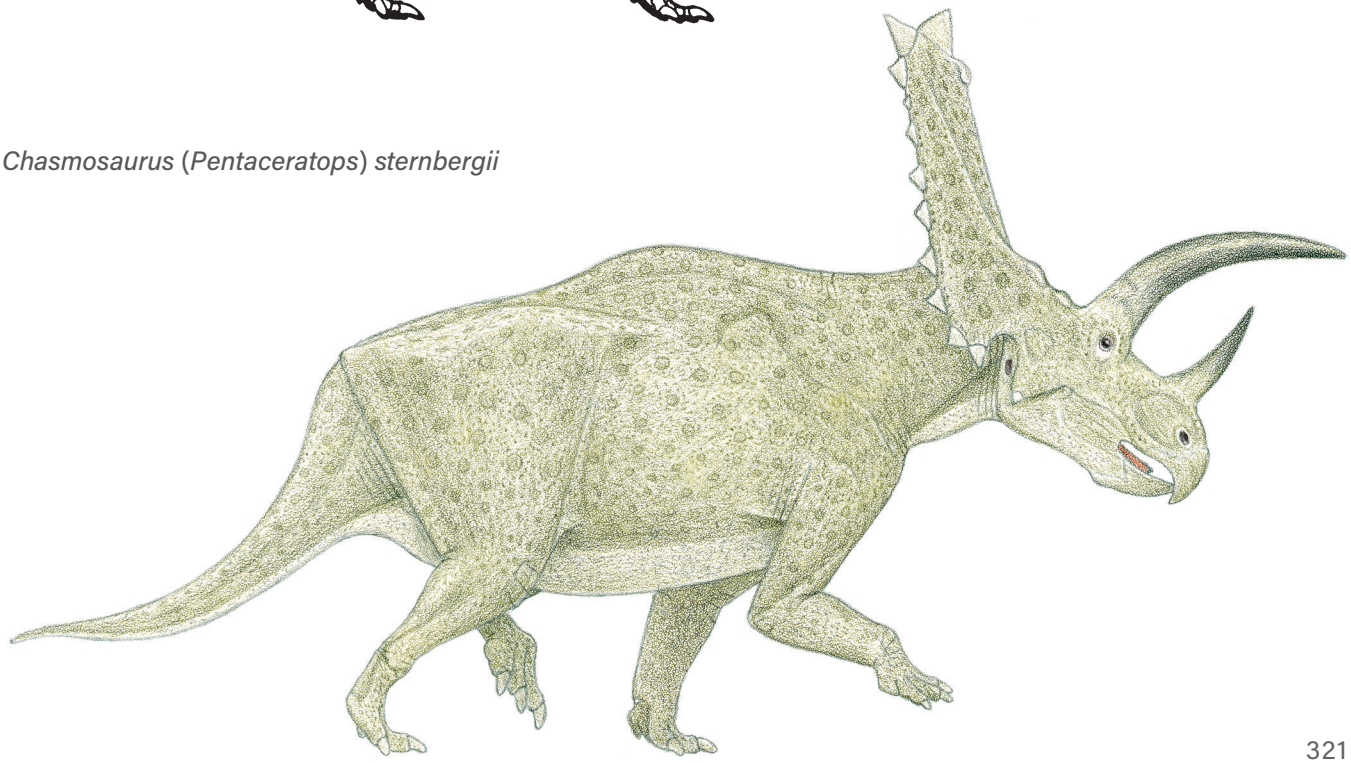
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Utah; lower to upper Kaiparowits.

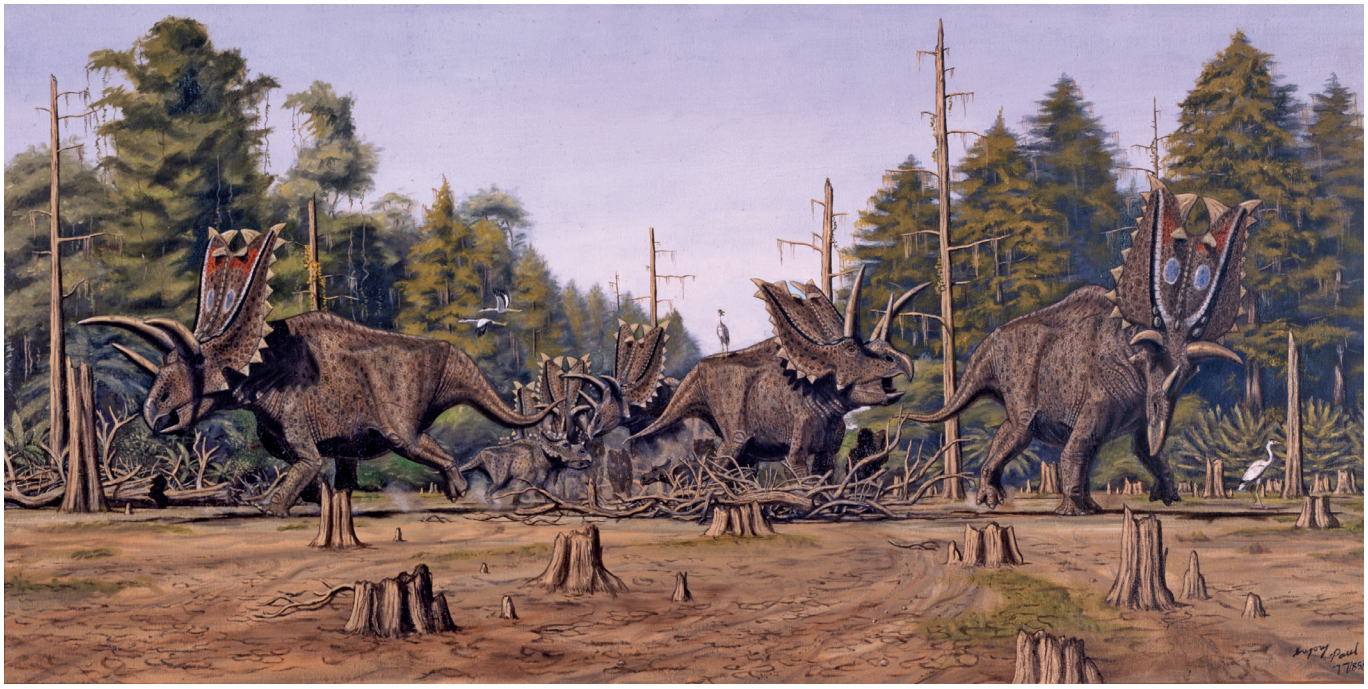
Chasmosaurus (*Pentaceratops*) *sternbergii*

— 5.5 m (18 ft) TL, 2.8 tonnes
FOSSIL REMAINS Several complete or partial skulls, a complete and some partial skeletons, completely known.
ANATOMICAL CHARACTERISTICS Nasal horn long, brow horns long, frill extremely elongated, tilted upward, back rim not broad, strongly indented, bearing large hornlets, innermost projecting vertically, small hornlets along side rims. Shoulder withers supported nuchal ligaments to neck and head. Belly broad, hind legs bowed.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; upper Fruitland, lower Kirtland.
HABITAT/S Moderately watered floodplain woodlands, coastal swamps and marshes.
NOTES Whether *Pentaceratops* is a distinct genus from *Chasmosaurus* that are very similar aside from horns and frills is problematic.

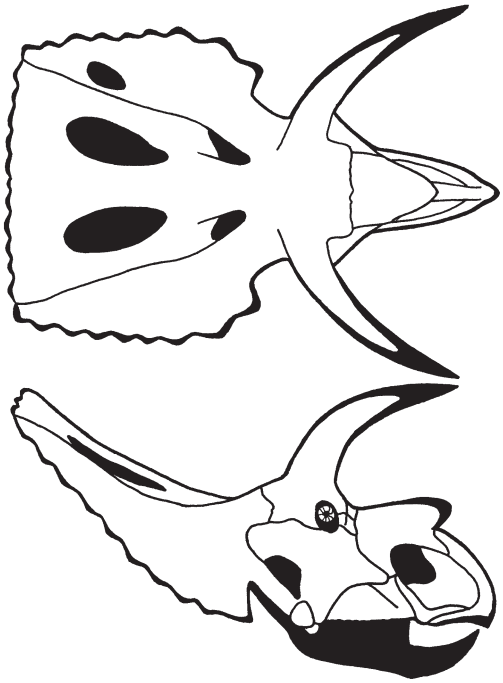


Chasmosaurus (*Pentaceratops*) *sternbergii*





Chasmosaurus (*Pentaceratops*) *sternbergii*



Anchiceratops? (= *Arrhinoceratops*) *brachyops*

Chasmosaurus (*Pentaceratops*) *froeseorum*

— 5.5 m (18 ft) TL, 2.5 tonnes
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Nasal horn short, brow horns long.
AGE Late Cretaceous, latest Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; upper Kirtland.
HABITAT/S Moderately watered floodplain woodlands, coastal swamps and marshes.
NOTES Called *Bisticeratops*, which does not appear sufficiently distinct from *Pentaceratops*.

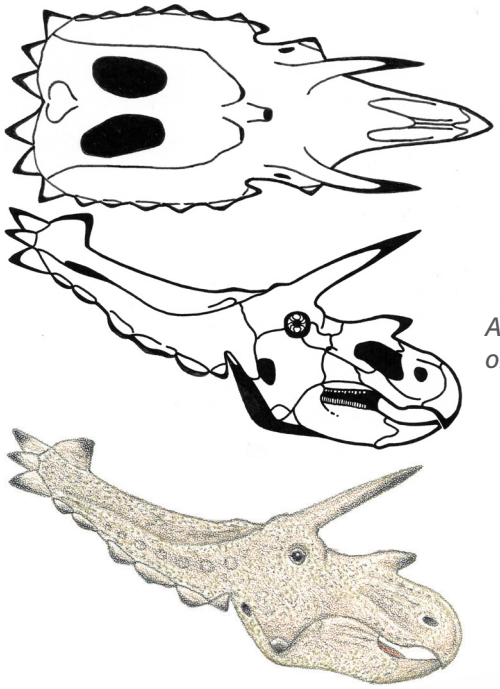
Anchiceratops? (= *Arrhinoceratops*) *brachyops*

— 4.5 m (15 ft) TL, 1.3 tonnes
FOSSIL REMAINS Two nearly complete skulls.
ANATOMICAL CHARACTERISTICS Nasal horn short, projects forward, brow horns long and directed sideways, frill subhorizontal, all hornlets small.
AGE Late Cretaceous, latest Campanian and earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower-middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be a gender morph of *Anchiceratops*.

Anchiceratops ornatus

— 4.5 m (15 ft) TL, 1.5 tonnes
FOSSIL REMAINS A few nearly complete skulls and minority of skeleton.

ANATOMICAL CHARACTERISTICS Nasal horn short, projecting forward, brow horns long to very long and directed sideways, frill subhorizontal, back rim not broad, large hornlets astride and atop centerline and along back, small hornlets on rim side.

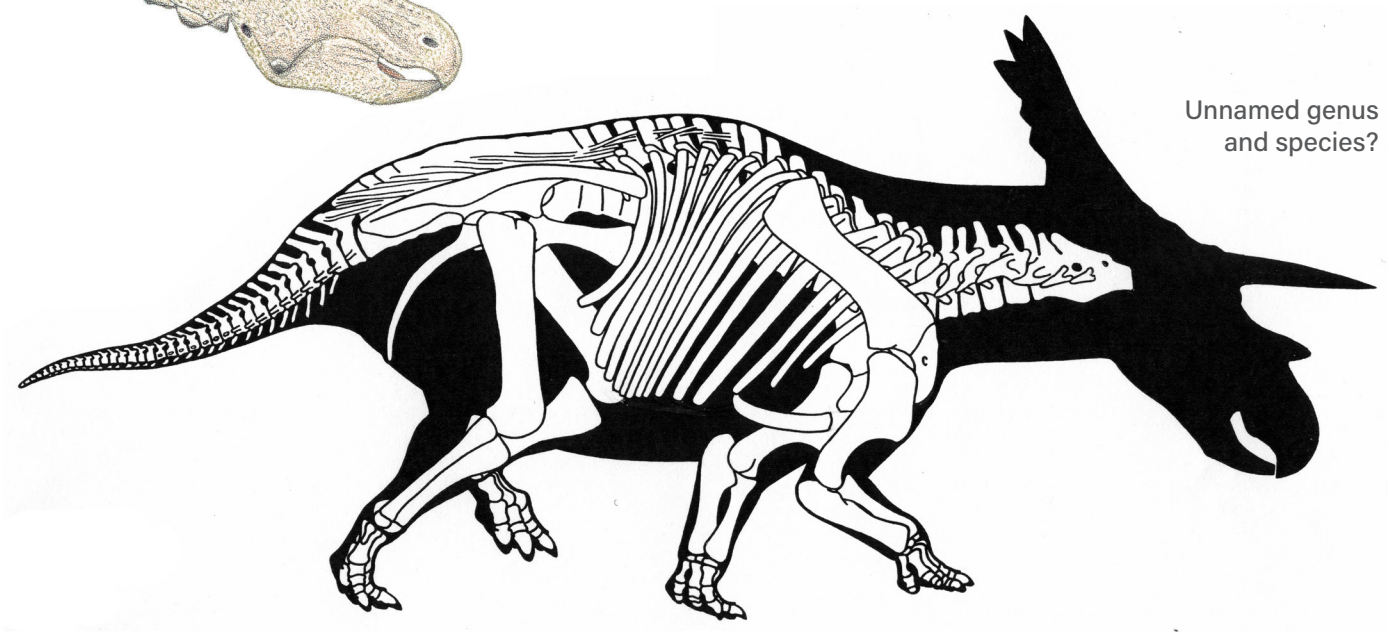


Anchiceratops ornatus

AGE Late Cretaceous, latest Campanian and earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower-middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Below complete skeleton no longer automatically attributed to this taxon.

Unnamed genus and species?

— 4.3 m (14 ft) TL, 1.3 tonnes
FOSSIL REMAINS Complete skeleton lacking skull.
ANATOMICAL CHARACTERISTICS Neck elongated. Arm robust.
AGE Late Cretaceous, latest Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower-middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Skeleton probably belongs to *Anchiceratops* or less common *Arrhinoceratops*, or may be a distinct taxon.



Unnamed genus and species?

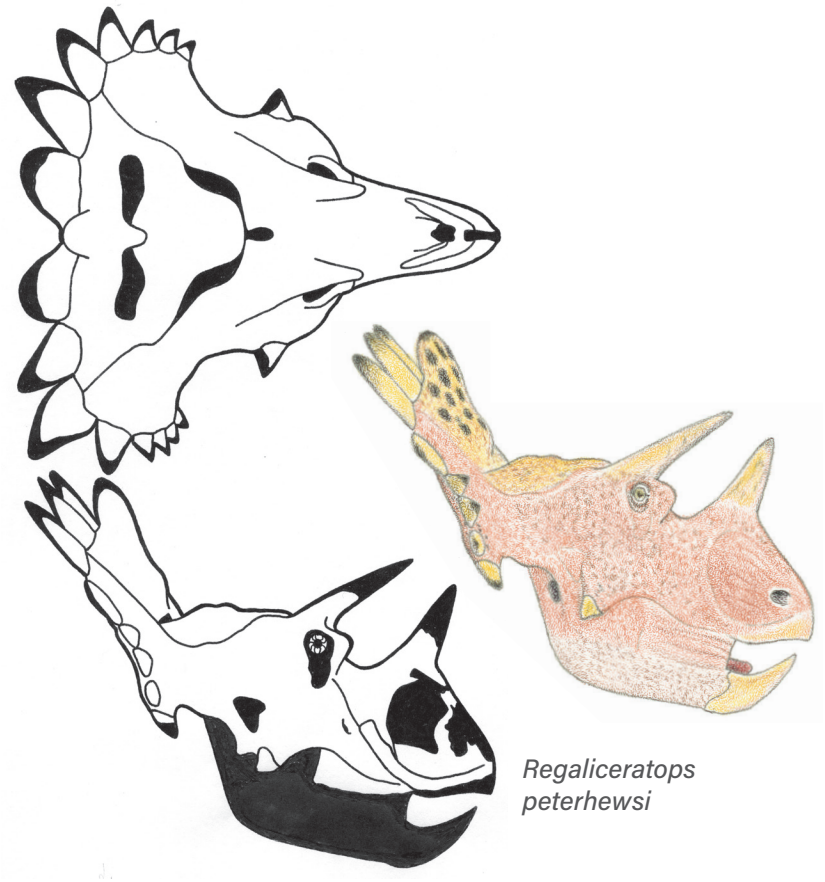
— TRICERATOPSINES

LARGE TO GIGANTIC CERATOPSIDS LIMITED TO THE LATE LATE CRETACEOUS OF NORTH AMERICA.

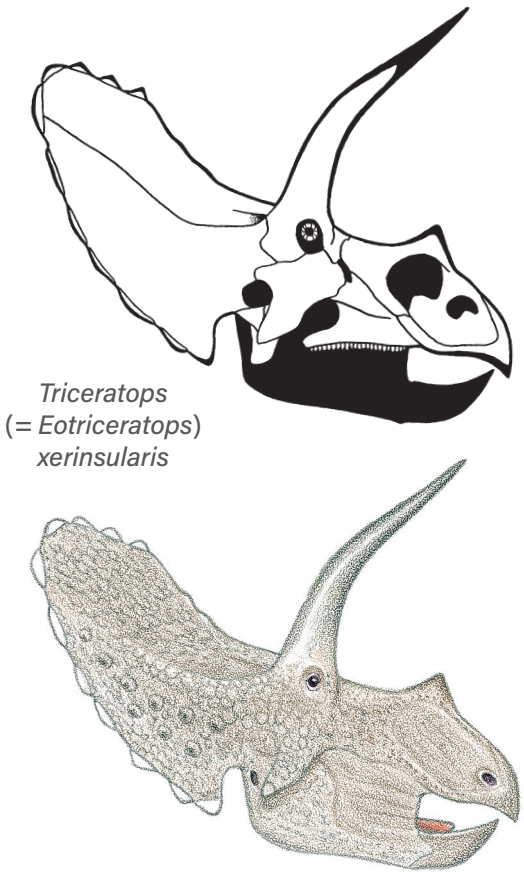
ANATOMICAL CHARACTERISTICS Pelvic ilia slope downward and backward, at least in *Triceratops*.

Regaliceratops peterhewsi

— 5 m (17 ft) TL, 2 tonnes
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Head and frill short, broad, nasal opening not elongated, nasal and brow horns short, frill openings small, rim adorned by large, stout hornlets, centerline boss on frill.
AGE Late Cretaceous, probably middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; probably upper Saint Mary River.



Regaliceratops peterhewsi



Triceratops (= Eotriceratops) xerinsularis

Titanoceratops ouranos

— 6.5 m (21 ft) TL, 5 tonnes

FOSSIL REMAINS Majority of skull and skeleton.

ANATOMICAL CHARACTERISTICS Nasal opening elongated, nasal horn short, brow horns long.

AGE Late Cretaceous, late Campanian.

DISTRIBUTION AND FORMATION/S New Mexico; upper Fruitland or lower Kirtland.

HABITAT/S Moderately watered floodplain woodlands, coastal swamps and marshes.

NOTES Originally placed in *Chasmosaurus* (*Pentaceratops*) *sternbergii*; uncertain anatomical features include length of frill, absence or presence of withers; orientation of pelvis precludes restoration.

Triceratops (= *Eotriceratops*) *xerinsularis*

— 8.5 m (28 ft) TL, 11 tonnes

FOSSIL REMAINS Complete skull and minority of skeleton.

ANATOMICAL CHARACTERISTICS Snout shallow, nasal opening elongated, nasal horn small, brow horns long, frill moderately elongated.

AGE Late Cretaceous, middle Maastrichtian.

DISTRIBUTION AND FORMATION/S Alberta; uppermost Horseshoe Canyon.

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

NOTES Largest known horned dinosaur, largest-headed known land animal. Separation of *Eotriceratops* from very similar *Triceratops*/*Torosaurus* not warranted because is more similar to *T. horridus* than latter is to *T. prorsus*; may include *Ojoceratops fowleri* from New Mexico—the latter is *Triceratops*; may be direct ancestor of *T. horridus*.

Triceratops horridus

— 8 m (25 ft) TL, 10 tonnes

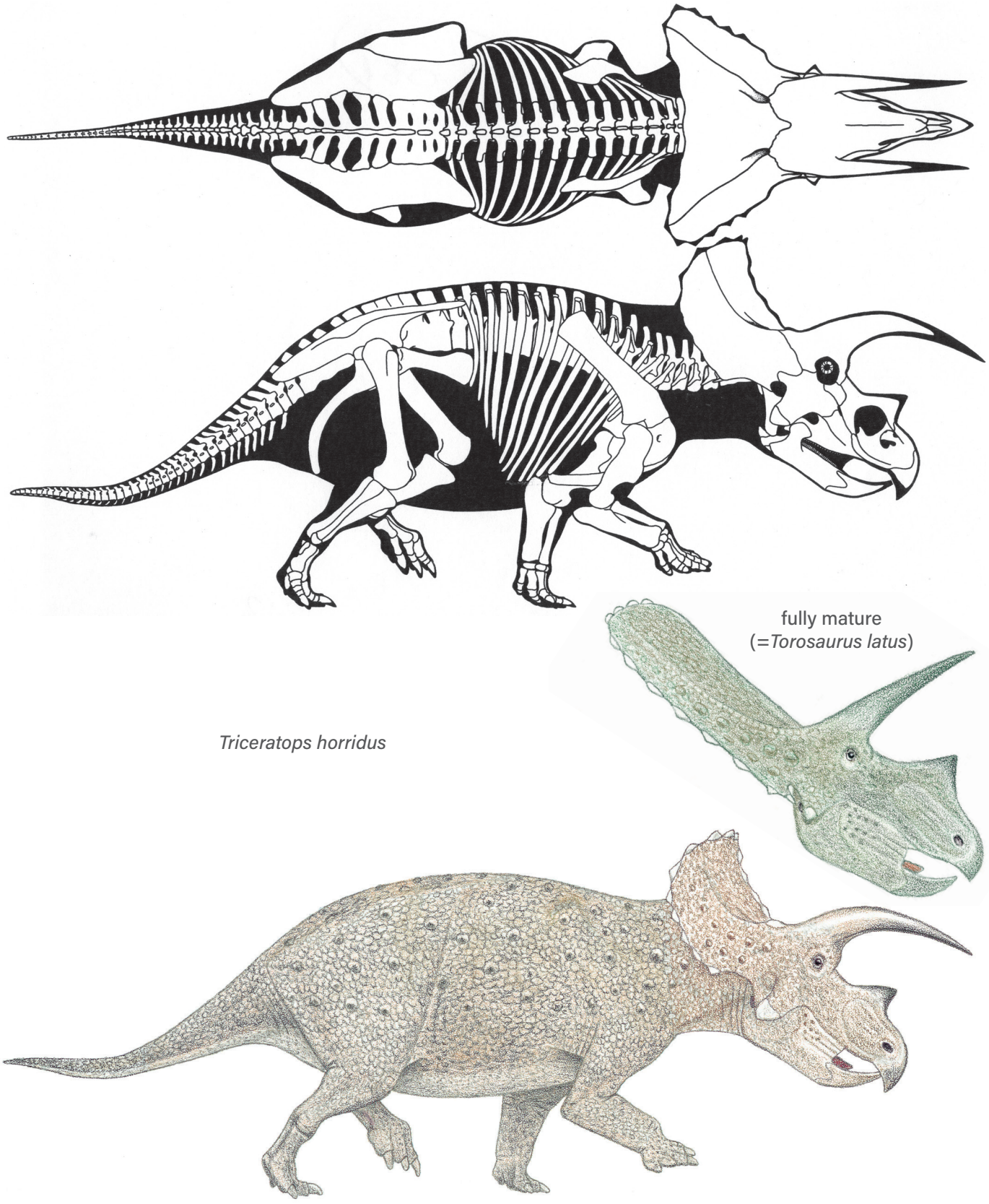
FOSSIL REMAINS Numerous skulls and some complete and partial skeletons including juveniles, completely known, skin traces.

ANATOMICAL CHARACTERISTICS Fairly variable. Snout shallow, nasal opening elongated, nasal horn quite small, brow horns long and project from well forward to past vertical, shift from arcing backward to forward with maturity; frill probably elongates greatly with maturity as large openings develop in at least one gender, hornlets suppressed and centerline hornlet lost. Skeleton very robust. Body scales generally larger than on other ceratopsids; largest often have raised cones and are widely spaced in an irregular pattern.

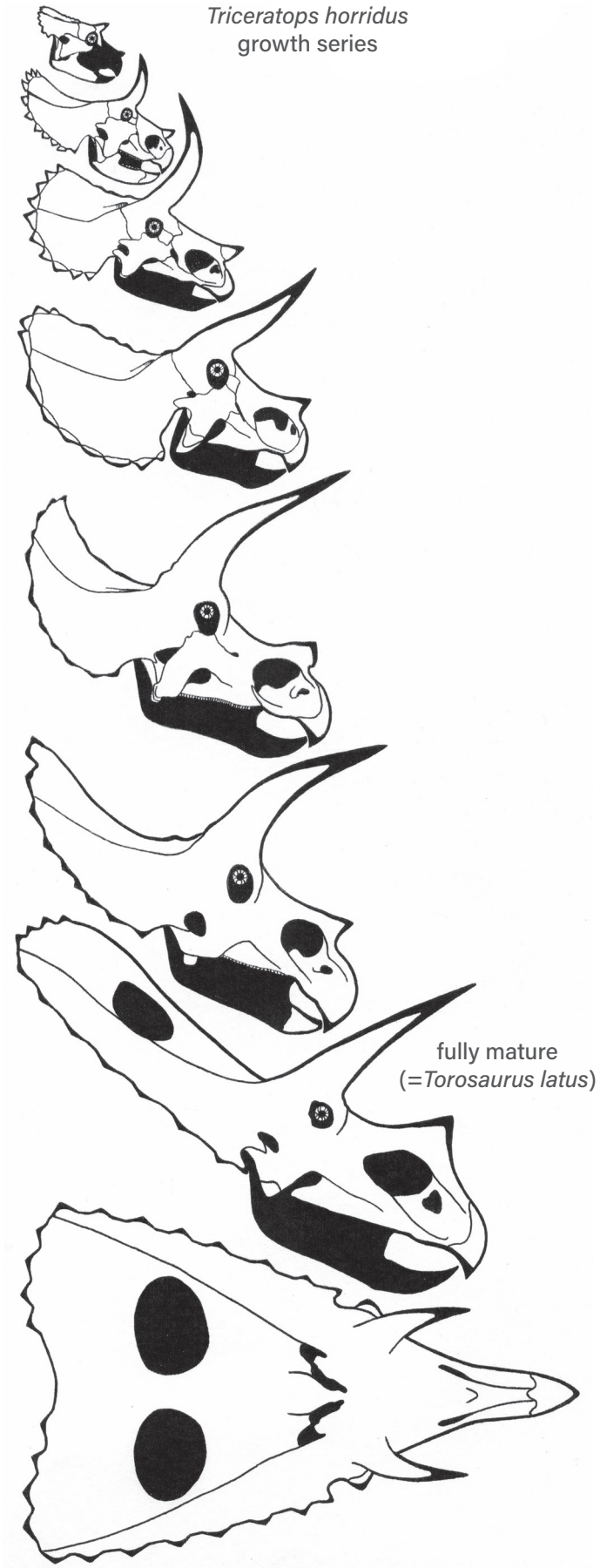
AGE Late Cretaceous, late Maastrichtian.

DISTRIBUTION AND FORMATION/S Dakotas, Wyoming, Montana; lower Lance and Hell Creek.

HABITAT/S Well-watered coastal woodlands, climate cooler than in latest Maastrichtian, possibly chilly in winter.



NOTES Probably includes *Nedoceratops* (= *Diceratops*) *hatcheri*, at least one adult gender (probably male) is probably *Torosaurus*—assignment of fragmentary remains from more southern regions to latter genus is problematic. Probably direct ancestor of *T.* unlabeled species.



Triceratops unlabeled species

— 8 m (25 ft) TL, 10 tonnes

FOSSIL REMAINS Some skulls.

ANATOMICAL CHARACTERISTICS Snout deep, nasal opening elongated, nasal horn small, brow horns quite long.

AGE Late Cretaceous, late Maastrichtian.

DISTRIBUTION AND FORMATION/S Dakotas, Wyoming, Montana; middle Lance and Hell Creek.

HABITAT/S Well-watered coastal woodlands.

NOTES Lacks an assigned species name because is possible that old, unused species name may apply to this taxon. Whether brow horns were always longer than those of *T. horridus* not certain. Probably direct ancestor of *T. prorsus.*

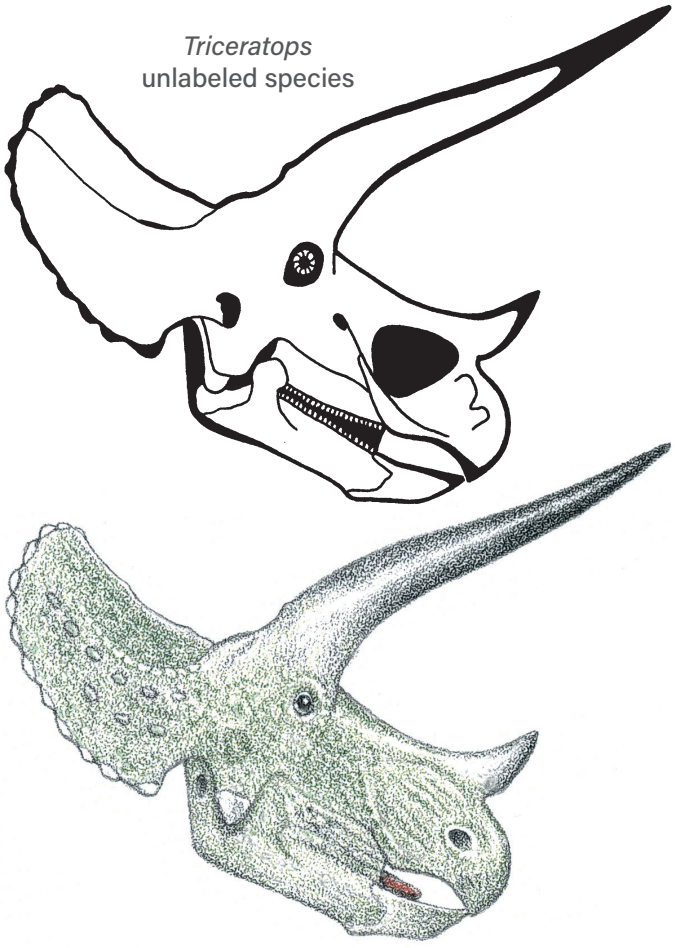
Triceratops prorsus

— 8 m (25 ft) TL, 10+ tonnes

FOSSIL REMAINS Numerous skulls and skeletal parts, bone beds.

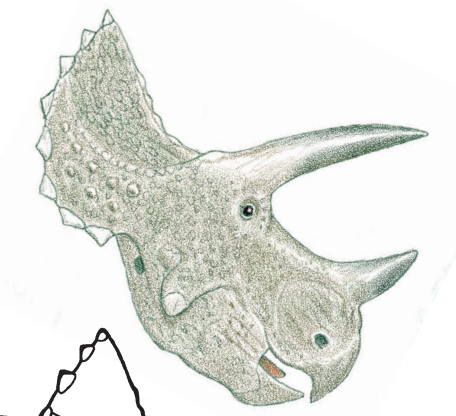
ANATOMICAL CHARACTERISTICS Fairly consistent. Snout deep, nasal opening elongated, nasal horn moderately long, brow horns moderately long, frill never elongated; openings develop and hornlets suppressed, centerline hornlet lost when fully mature. Skeleton very robust.

AGE Late Cretaceous, latest Maastrichtian.



DISTRIBUTION AND FORMATION/S Montana, Wyoming, Alberta, Saskatchewan; upper Lance and Hell Creek, Denver, Laramie, Scollard, Frenchman.
HABITAT/S Well-watered coastal woodlands, climate warmer than earlier in Maastrichtian.
HABITS A bitten-off and healed brow horn confirms aggressive defensive head-to-head combat with its main enemy, *Tyrannosaurus*.
NOTES *Triceratops* was most common large herbivore in the sediments, making up two-thirds of the population.

Triceratops prorsus



— ORNITHOPODS

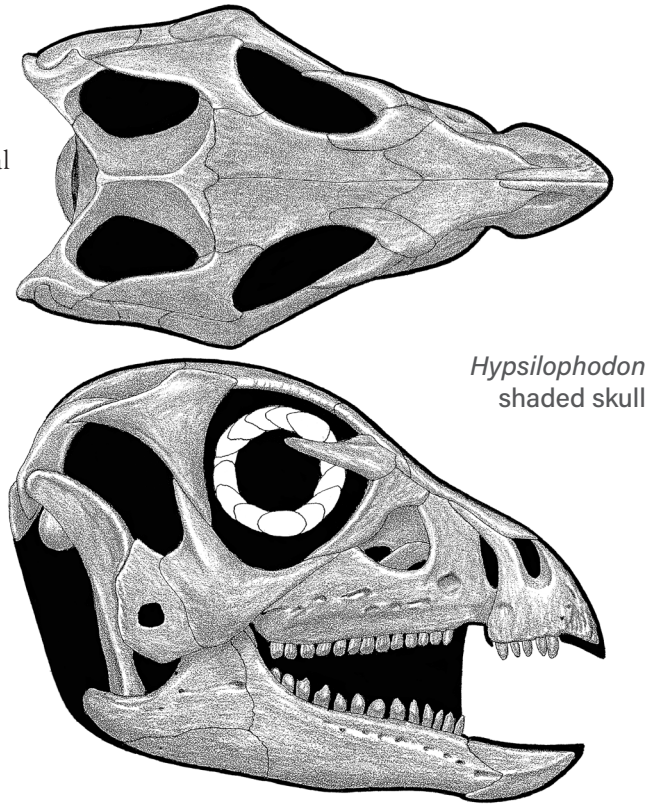
SMALL TO GIGANTIC GENASAUR ORNITHISCHIANS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads not greatly enlarged, beaks not hooked, eyes large, main tooth rows well developed. Necks S-curved. Trunks and tails stiffened by ossified tendons. Tails moderately long. Strongly bipedal to semiquadrupedal, arms and legs flexed, and latter always long, so good runners. Fingers five to four. Toes four to three. Rib-free lumbar region in front of hips implies a mammal-like diaphragm was present. Large examples scaly; integument of smaller examples uncertain but may have been insulated with fibers.
ONTOGENY Growth rates apparently rapid in at least some examples.
HABITAT/S Very variable, from tropics to polar winters, from arid to wet.
HABITS Low- to medium-level browsers; some species may have fed in shallow water on occasion. Main defense running, also kicking with feet among medium-sized and larger species. Competent surface swimmers so able to cross large bodies of water, some diving ability.
NOTES The kangaroos, deer, antelope, and cattle of the last half of the Mesozoic, and the most common herbivores of the Cretaceous.

— "HYPSILOPHODONTS"

SMALL TO MEDIUM-SIZED ORNITHOPODS OF THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

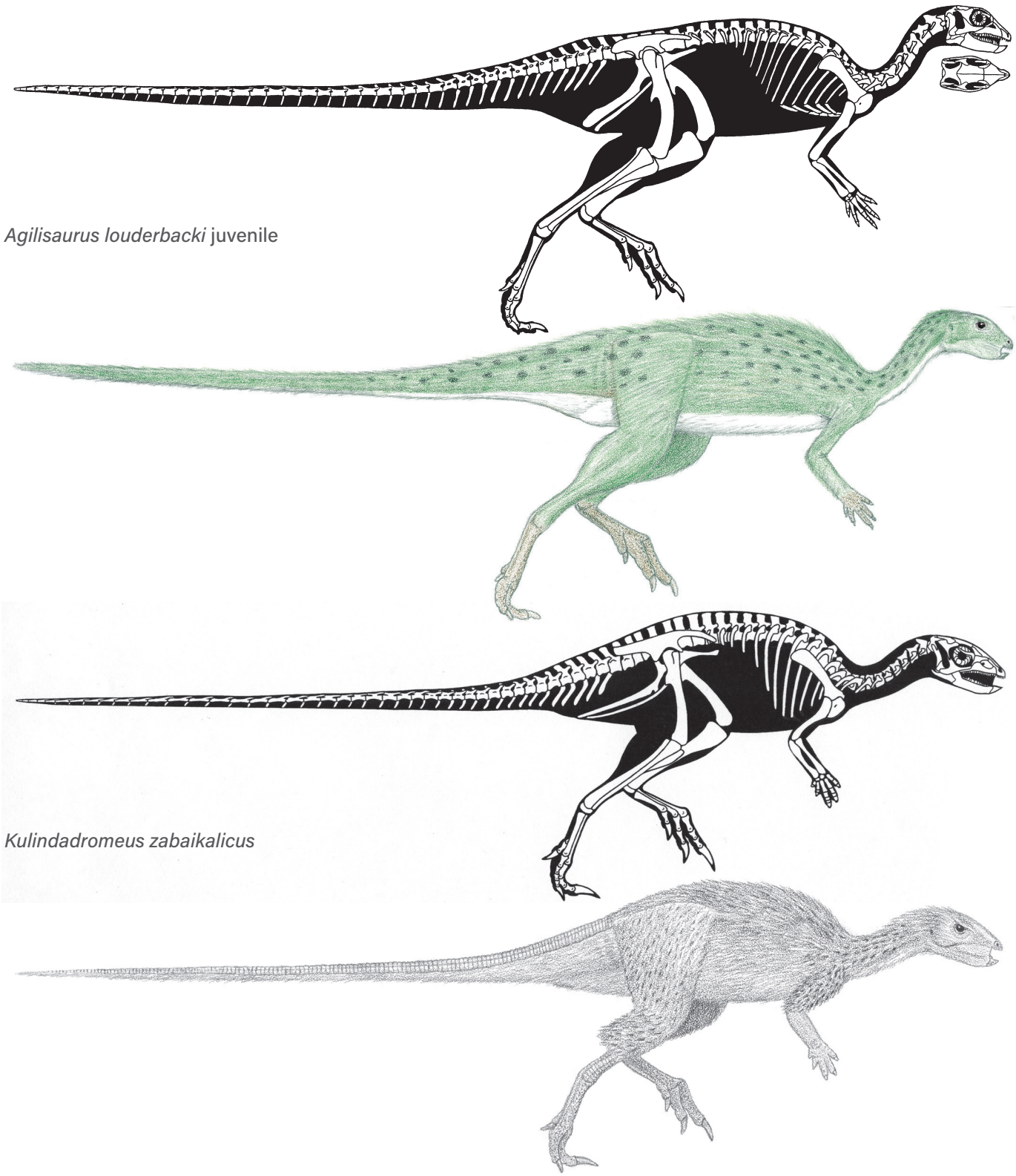
ANATOMICAL CHARACTERISTICS Uniform. Heads subtriangular, narrow, beaks narrow, eyes shaded by overhanging rim, teeth under upper beaks, main tooth rows well developed. Trunks and hips fairly narrow, large interrib plates in at least some examples. Tails moderately long. Bipedal except could move quadrupedally at slow speeds. Arms fairly short, so strongly bipedal; hands small, five grasping fingers tipped with small claws. Legs long and usually fairly gracile, so speed potential high, four long toes tipped with blunt claws.
HABITAT/S Very variable, from tropics to polar winters, from arid to wet.
HABITS Low-level browsers and omnivores that picked up insects and small vertebrates. Predominantly terrestrial, probably some climbing ability, well-developed shoulders indicate burrowing ability. Main defense high speed.
NOTES Closest living analogues small kangaroos, deer, and antelope. Burrows attributable to small ornithopods have been found in North America and then-polar Australia. The relationships of these generalized-grade ornithopods are problematic: possibly but not certainly a unified group, and splittable into a number of divisions. Fragmentary Late Cretaceous *Morrosaurus antarcticus* shows presence in Antarctica. Gastroliths found with some examples.



Hypsilophodon shaded skull

Yandusaurus hongheensis or *Agilisaurus louderbacki*

— 3.8 m (12 ft) TL, 150 kg (300 lb)
FOSSIL REMAINS Two nearly complete skulls and skeletons and partial remains, adult and juvenile.
ANATOMICAL CHARACTERISTICS Head small, four teeth under upper beak, a few large bladed teeth near front of lower jaws. End of tail fairly deep.
AGE Late Jurassic, probably Bathonian.
DISTRIBUTION AND FORMATION/S Central China; lower Xiashaximiao.
HABITAT/S Heavily forested.
HABITS Bladed teeth facilitated handling small prey items.
NOTES *A. louderbacki* and *Hexinlusaurus multidens* probably immature examples of this species, but the original fossil of *Y. hongheensis* is very incomplete and much larger than the others, so the first name may be most valid.



Agilisaurus louderbacki juvenile

Kulindadromeus zabaikalicus

Kulindadromeus zabaikalicus

— 1 m (3.3 ft) TL, 2.5 kg (5 lb)

FOSSIL REMAINS Numerous partial skulls and skeletons, scales, extensive fibers.

ANATOMICAL CHARACTERISTICS Much of body covered by short, coarse and fine filaments, latter long on upper shank; small, rounded, nonoverlapping scales on hands and feet, rows of large overlapping scales on upper half of tail.

AGE Middle Jurassic, Bathonian.

DISTRIBUTION AND FORMATION/S Southern Siberia; lower Ukureyskaya.

HABITAT/S Woodlands and lakes.
NOTES Geological age not certain.

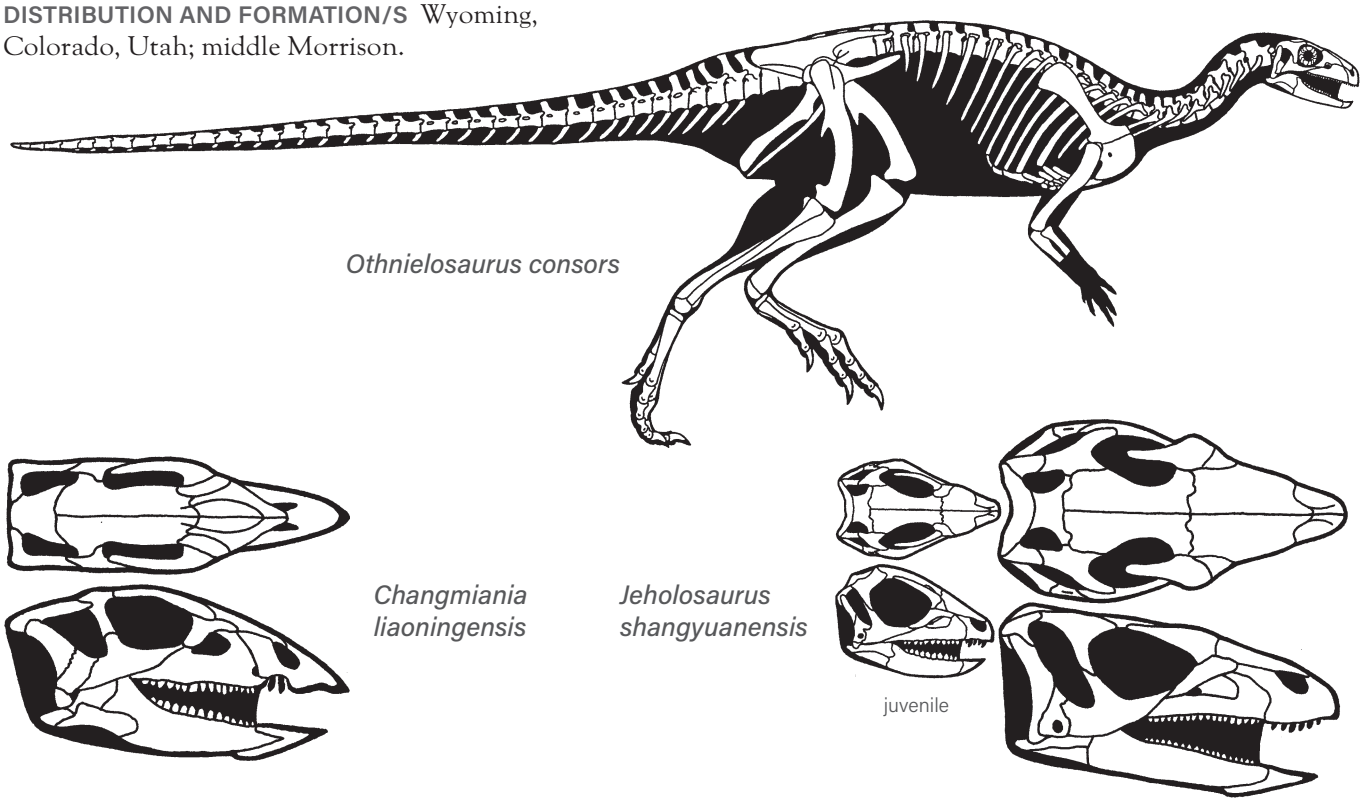
Minimocursor phunoiensis
— 1.2 m (4 ft) TL, 4 kg (9 lb)
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Shoulder girdle small.
AGE Late Jurassic?
DISTRIBUTION AND FORMATION/S Thailand; lower Phu Kradung.
NOTES Geological age not certain.

Drinker nisti
— 2 m (6.5 ft) TL, 25 kg (55 lb)
FOSSIL REMAINS Partial skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Jurassic, late middle and/or late Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; upper Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Othnielosaurus consors
— 2.2 m (7.5 ft) TL, 33 kg (60 lb)
FOSSIL REMAINS Complete skull and majority of skeletons.
ANATOMICAL CHARACTERISTICS Head small, subrectangular, four teeth under upper beak.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming, Colorado, Utah; middle Morrison.
HABITAT/S Wetter than earlier Morrison, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Once *Othnielia rex*, which is based on inadequate remains; it is uncertain whether the skull and the skeleton illustrated here belong to this species or to one or two other taxa.

Changmiania liaoningensis
— 1.2 m (3.5 ft) TL, 5 kg (10 lb)
FOSSIL REMAINS Two nearly complete skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head fairly long and low, snout sharp pointed, two large teeth under back of upper beak.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
NOTES Lack of side views of skeletons currently precludes their restoration.

Jeholosaurus shangyuanensis
— 1.3 m (4 ft) TL, 6 kg (12 lb)
FOSSIL REMAINS Skulls and partial skeletons, adult to juvenile.
ANATOMICAL CHARACTERISTICS Head long, low, snout robust, five robust teeth under upper beak.
AGE Early Cretaceous, at least latest Barremian.
DISTRIBUTION AND FORMATION/S Northeastern China; lower Yixian.



HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.

Changchunsaurus parvus

— 1.5 m (5 ft) TL, 10 kg (20 lb)
FOSSIL REMAINS Majority of distorted skull and uncertain part of skeleton.
ANATOMICAL CHARACTERISTICS Head shallow, upper and lower beaks pointed.
AGE Late Early Cretaceous or early Late Cretaceous.
DISTRIBUTION AND FORMATION/S Northeastern China; Quantou.
HABITAT/S Well-watered forests and lakes, winters chilly with snow.

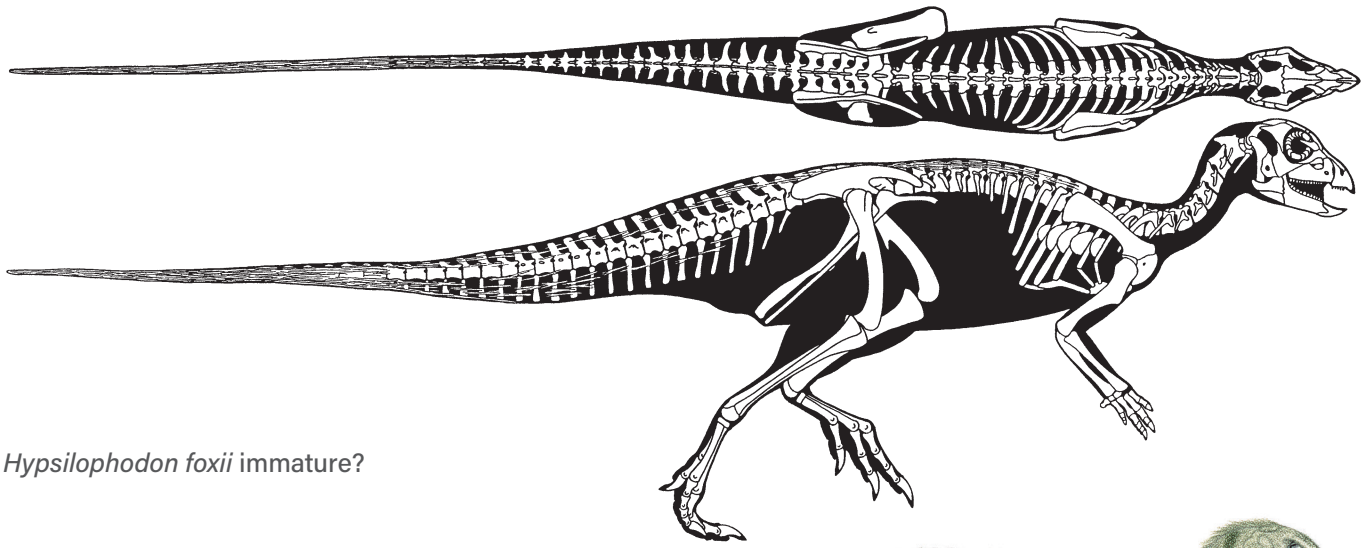
Haya griva

— 1.6 m (5 ft) TL, 12 kg (25 lb)
FOSSIL REMAINS A few complete to partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head low, five large teeth under upper beak.
AGE Late Cretaceous, probably Santonian.
DISTRIBUTION AND FORMATION/S Mongolia; Javkhlant.

Hypsilophodon foxii

— 2 m (6.5 ft) TL, 23 kg (50 lb)
FOSSIL REMAINS About a dozen complete and partial skulls and skeletons, juvenile to adult, completely known.
ANATOMICAL CHARACTERISTICS Five teeth under upper beak.

Haya griva



Hypsilophodon foxii immature?

AGE Early Cretaceous, late Barremian.
DISTRIBUTION AND FORMATION/S Southern England; uppermost Wessex.
NOTES The classic hypsilophodont.

Convolosaurus marri
— 2.5 m (8 ft) TL, 50 kg (100 lb)
FOSSIL REMAINS Skulls and skeletal remains of varying completeness, juvenile to adult.
ANATOMICAL CHARACTERISTICS Head deep, rounded, four teeth under upper beak.
AGE Early Cretaceous, lower or middle Aptian.
DISTRIBUTION AND FORMATION/S Texas; lower Twin Mountains.
HABITAT/S Semiarid coastal floodplain.
NOTES Congregation of individuals of varying ages may indicate social behavior.

Convolosaurus marri

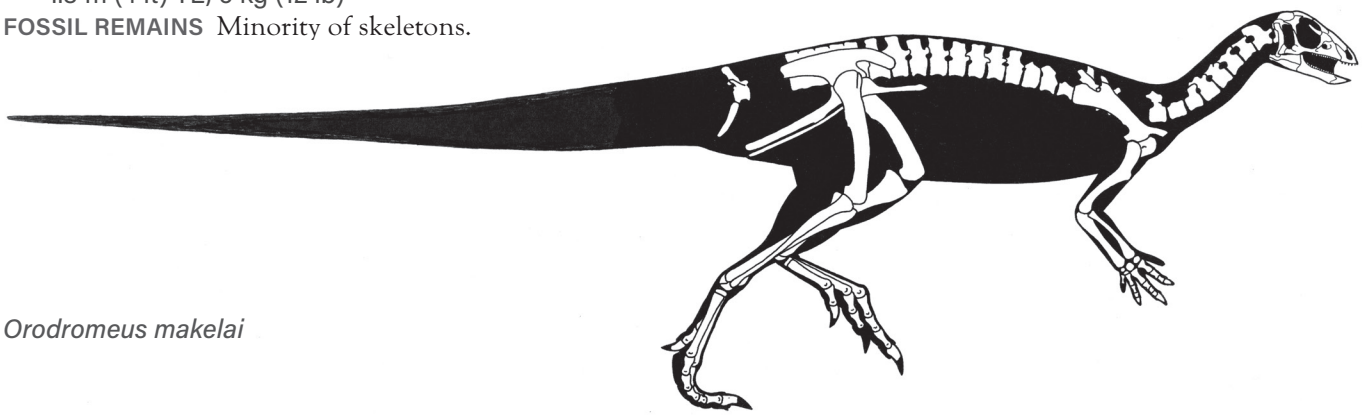
Leaellynasaura amicagraphica
— 3 m (10 ft) TL, 90 kg (200 lb)
FOSSIL REMAINS Minority of skull and possible skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Albian.
DISTRIBUTION AND FORMATION/S Southern Australia; Eumeralla.
HABITAT/S Polar forests with warm, daylight-dominated summers and cold, dark winters.
NOTES Only skull fragment may belong to species, or may include *Diluvicursor pickeringi*. Large orbits of a possible fossil considered evidence of nocturnal habits are instead a juvenile characteristic.

Fulgurotherium australe
— 1.3 m (4 ft) TL, 6 kg (12 lb)
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Southeastern Australia; Griman Creek.
HABITAT/S Polar forests with warm, daylight-dominated summers and cold, dark winters.

Zephyrosaurus schaffi
—2 m (6.5 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Partial skulls and small portion of two skeletons.
ANATOMICAL CHARACTERISTICS Upper beak strengthened.
AGE Early Cretaceous, middle Albian.
DISTRIBUTION AND FORMATION/S Montana, Wyoming; upper Cloverly.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
HABITS Strengthening of snout indicates burrowing.

Oryctodromeus cubicularis
—2 m (7 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Minority of skulls and skeletons, juveniles and adult, burrows.
ANATOMICAL CHARACTERISTICS Upper beak strengthened. Shoulder blade exceptionally enlarged. Pelvis strengthened.
AGE Late Cretaceous, Cenomanian.
DISTRIBUTION AND FORMATION/S Montana; Blackleaf.
HABITAT/S Seasonally dry upland woodlands.
HABITS Dug sinuous burrows a few meters long with strengthened beak and arms while bracing with legs.

Orodromeus makelai
—Adult size uncertain
FOSSIL REMAINS A number of partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Upper beak strengthened, large boss on cheek, five teeth under upper beak. Shoulder blade exceptionally enlarged.
AGE Late Cretaceous, late middle Campanian.



Orodromeus makelai

DISTRIBUTION AND FORMATION/S Montana; middle Two Medicine.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes and drier upland woodlands.
HABITS Strengthening of snout and arms indicates well-developed burrower.

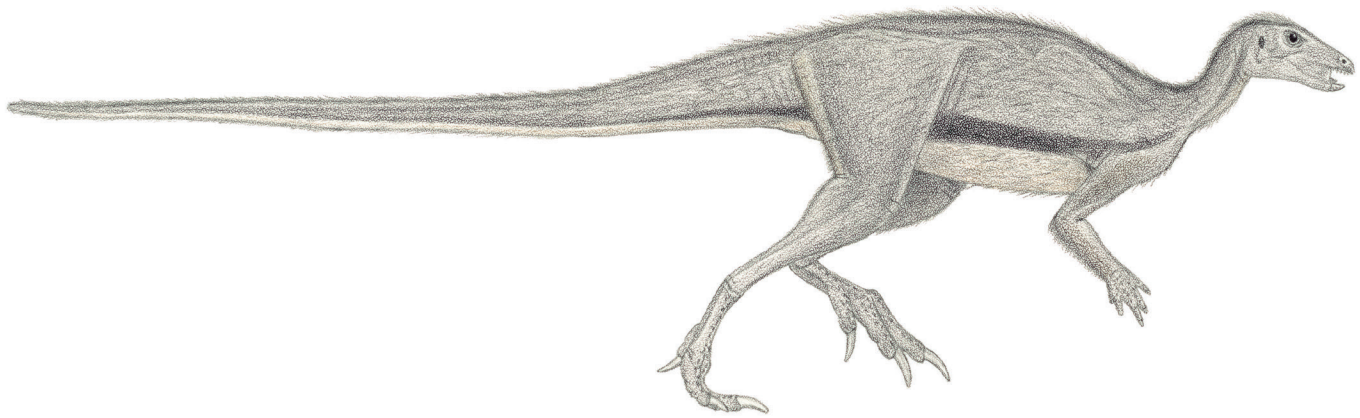
Koreanosaurus boseongensis
— Adult size uncertain
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Shoulder blade exceptionally enlarged.
AGE Late Cretaceous, Santonian or Campanian.
DISTRIBUTION AND FORMATION/S North Korea; Seonso.
HABITS Strengthening of snout and arms indicates well-developed burrower.

Parksosaurus warreni
— 2.5 m (8 ft) TL, 47 kg (100 lb)
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Shoulder blade exceptionally enlarged, arm robust. Toes unusually long.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Long toes imply *Parksosaurus* was adapted for moving on soft soils near watercourses and in marshlands. Strong shoulders and arms indicate burrowing.

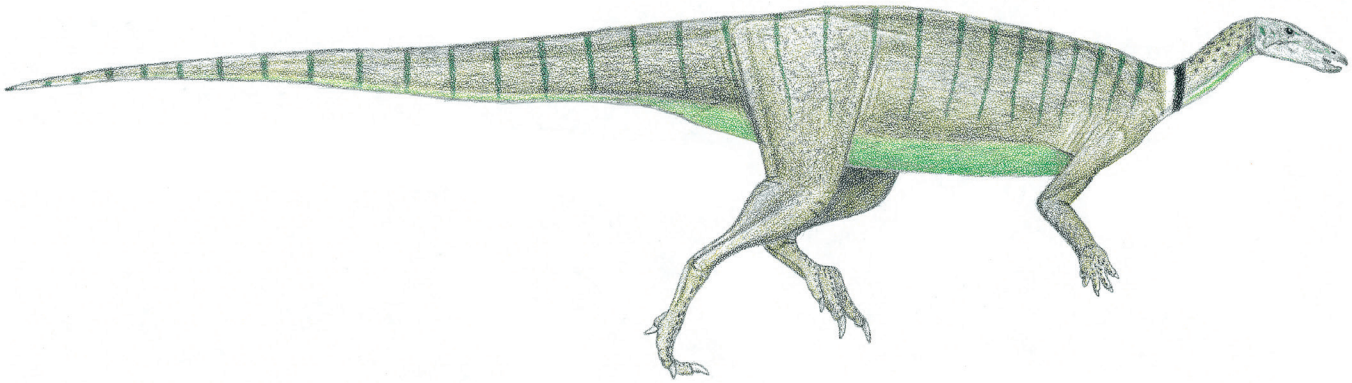
Thescelosaurus neglectus (see p.334)
— 3 m (10 ft) TL, 90 kg (200 lb)
FOSSIL REMAINS A few complete and partial skulls and skeletons, completely known.
ANATOMICAL CHARACTERISTICS Head small, long, shallow in part because beak is long, four teeth under upper beak. Shoulder blade enlarged, arm robust.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming, South Dakota; Lance, Hell Creek, Laramie.
HABITAT/S Well-watered coastal woodlands.
HABITS Strong shoulders and arms indicate burrowing.
NOTES May include *T. garbanii* and *Bugenasaura infernalis*.

Thescelosaurus assiniboiensis
— Adult size uncertain
FOSSIL REMAINS Partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Shoulder blade enlarged, arm robust.
AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Saskatchewan; Frenchman.

Parksosaurus warreni



Thescelosaurus neglectus



HABITAT/S Well-watered coastal woodlands.
HABITS Strong shoulders and arms indicate burrowing.
NOTES May be direct descendant of *T. neglectus*.

Gasparinisaura cincosaltensis

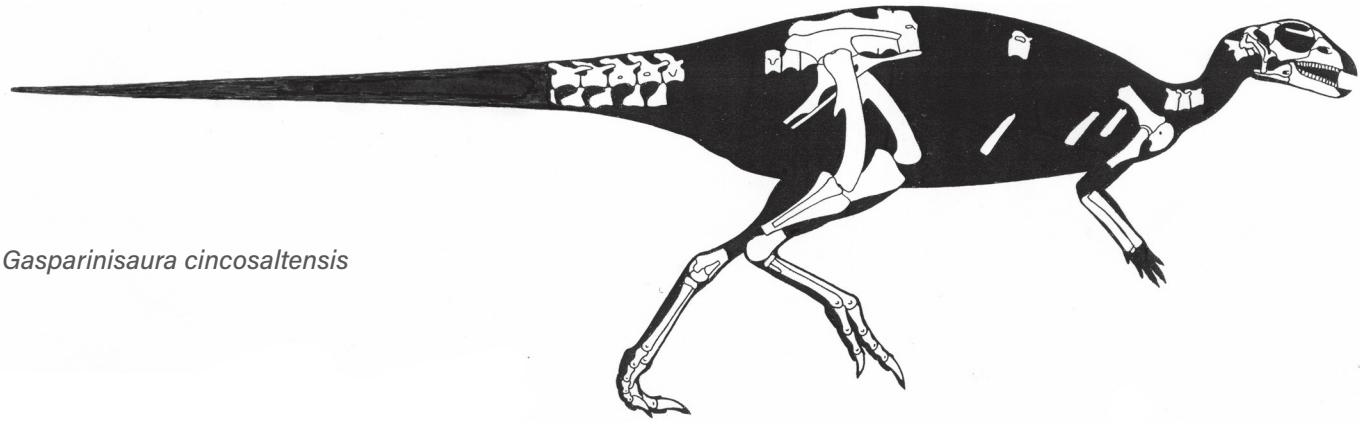
— 1.7 m (5.5 ft) TL, 16 kg (35 lb)
FOSSIL REMAINS Partial skull and skeletons, juvenile to adult.
ANATOMICAL CHARACTERISTICS Standard for type.
AGE Late Cretaceous, late Santonian or early Campanian.
DISTRIBUTION AND FORMATION/S Western Argentina; Anacleto.
HABITAT/S Seasonally semiarid.

Isasicursor santacrucensis

— 4.5 m (15 ft) TL, 250 kg (550 lb)
FOSSIL REMAINS Partial remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; upper Chorrillo.

Notohypsilophodon comodorensis

— 1.3 m (4 ft) TL, 6 kg (12 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.

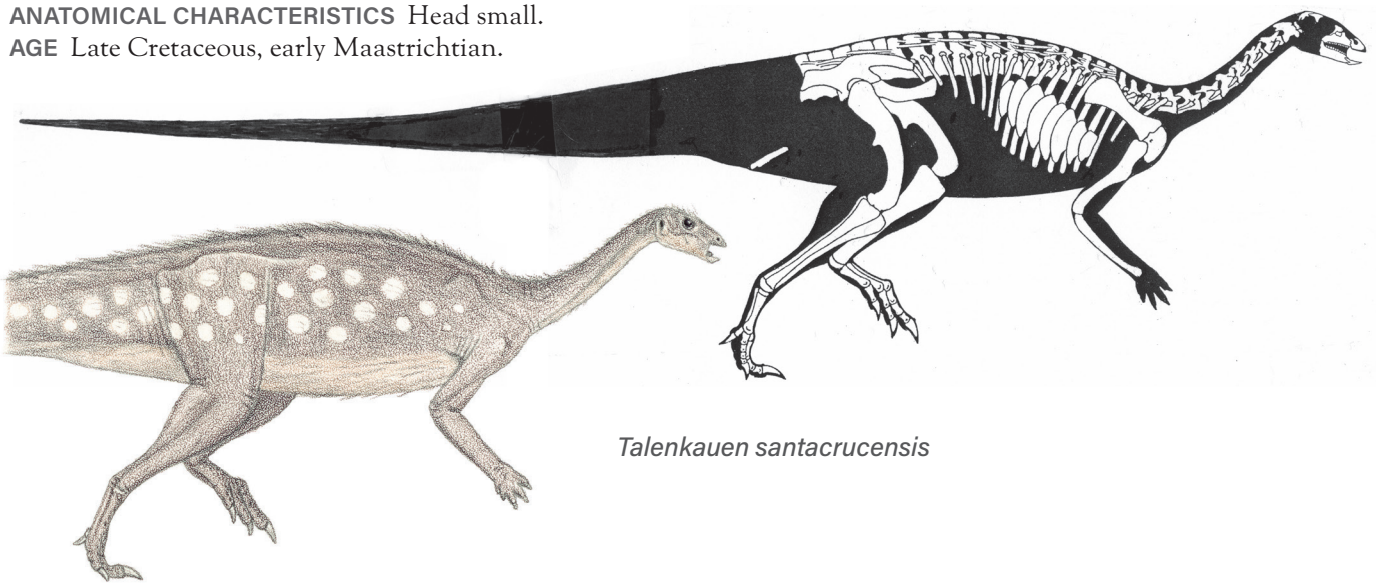


Gasparinisaura cincosaltensis

Macrogryphosaurus gondwanicus
— 5 m (16 ft) TL, 300 kg (650 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Portezuelo.
HABITAT/S Well-watered woodlands with short dry season.

Talenkauen santacrucensis
— 4.7 m (15 ft) TL, 325 kg (650 lb)
FOSSIL REMAINS Partial skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head small.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Argentina; Pari Aike.

Anabisetia saldiviai
— 2 m (6.5 ft) TL, 20 kg (45 lb)
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian or early Turonian.
DISTRIBUTION AND FORMATION/S Western Argentina; Lisandro.
HABITAT/S Well-watered woodlands with short dry season.



Talenkauen santacrucensis

— IGUANODONTIANS

SMALL TO GIGANTIC ORNITHOPODS FROM THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, MOST CONTINENTS.

ANATOMICAL CHARACTERISTICS No teeth under upper beak. Strongly bipedal to semiquadrupedal. Five to four fingers. Four to three toes.
HABITAT/S Very variable, from sea level to highlands, from tropics to polar winters, from arid to wet.
NOTES Absence from Antarctica probably reflects lack of sufficient sampling.

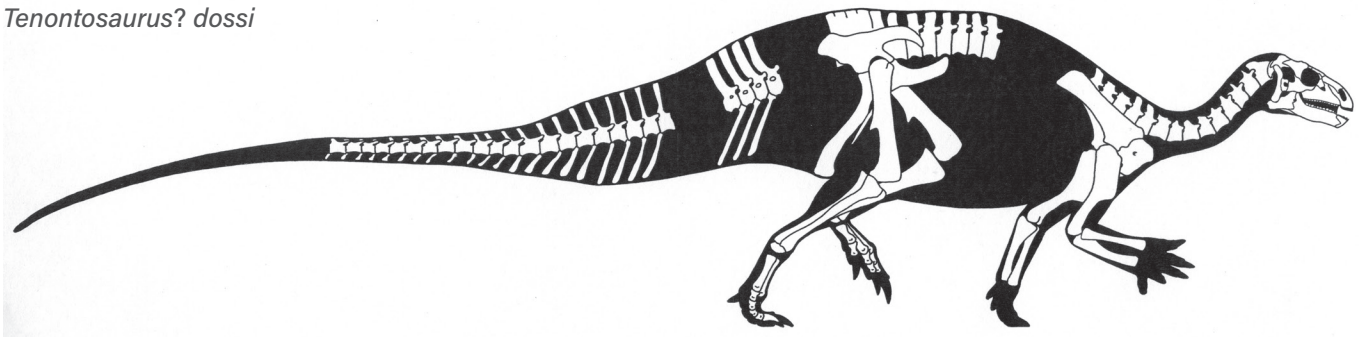
— TENONTOSAURS

LARGE IGUANODONTIANS LIMITED TO THE LATE EARLY CRETACEOUS OF NORTH AMERICA.

ANATOMICAL CHARACTERISTICS Heads narrow, beaks narrow, lower beak edges serrated, snouts elongated, nasal openings enlarged, eyes shaded by overhanging rim. Trunks and hips fairly narrow. Tails long, bases very deep. Trunk vertebral series downcurved and arms moderately long, so semiquadrupedal; hands short, broad, five grasping fingers tipped with small claws. Four long toes tipped with blunt claws.
HABITS Low- and medium-level browsers.

Tenontosaurus? *dossi*
— 7 m (23 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Texas; middle Twin Mountains.
HABITAT/S Semiarid coastal floodplain.

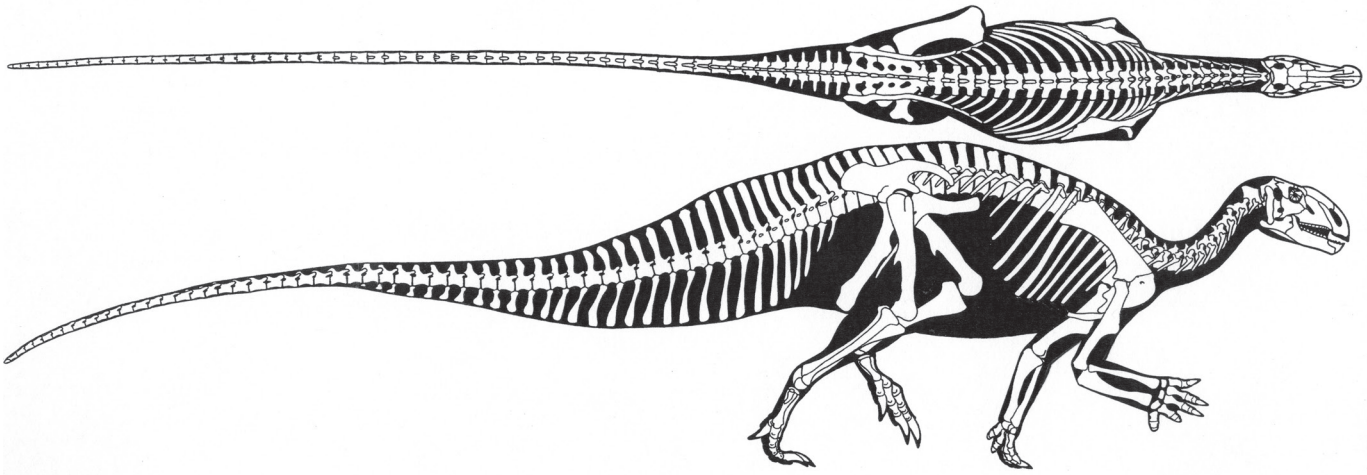
Tenontosaurus? *dossi*



NOTES Whether this is the same genus as later *T. tilletti* is problematic.

Tenontosaurus tilletti

— 6 m (20 ft) TL, 630 kg (1,400 lb)
FOSSIL REMAINS Numerous complete and partial skulls and skeletons, completely known.
ANATOMICAL CHARACTERISTICS Head including snout deep, subrectangular.
AGE Early Cretaceous, middle Albian.
DISTRIBUTION AND FORMATION/S Montana, Wyoming, Texas; upper Cloverly, Paluxy.
HABITAT/S Semiarid floodplains to coastal.



Tenontosaurus tilletti

— RHABDODONTS

MEDIUM-SIZED TO LARGE IGUANODONTIANS LIMITED TO THE CRETACEOUS OF EUROPE AND AUSTRALIA.

ANATOMICAL CHARACTERISTICS Heads subtriangular in top view, beaks narrow, eyes shaded by overhanging rim, lower jaws deep, teeth large. Skeletons heavily constructed. Trunks and hips fairly broad. Arms fairly short. Long toes tipped with blunt claws. Bipedal except could move quadrupedally at slow speeds.
HABITS Low- and medium-level browsers, broad aft skull indicates powerful jaw muscles, probably able to feed on coarse vegetation.
NOTES Absence from other continents reflects insufficient sampling.

Muttaburrasaurus langdoni

Muttaburrasaurus langdoni

— 8 m (25 ft) TL, 2.9 tonnes
FOSSIL REMAINS Majority of skulls and partial skeleton.
ANATOMICAL CHARACTERISTICS Head rather small, long, fairly shallow and broad; the latter indicates jaw muscles more powerful than in other ankylopollexians, snout elongated, low bulbous crest over snout, nostrils face upward, main teeth rows form slicing batteries. Arm moderately long, so semiquadrupedal.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Northeastern Australia; Mackunda.
HABITS Possibly omnivores that scavenged carcasses.
NOTES Has been considered a relative of camptosaurs, less plausibly rhabdodonts.

Fostoria dhimbangunmal

— 4.5 m (15 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Partial skull and skeletal remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Eastern Australia; upper Griman Creek.
NOTES Has been considered a relative of camptosaurs and less plausibly rhabdodonts.

Rhabdodon priscus

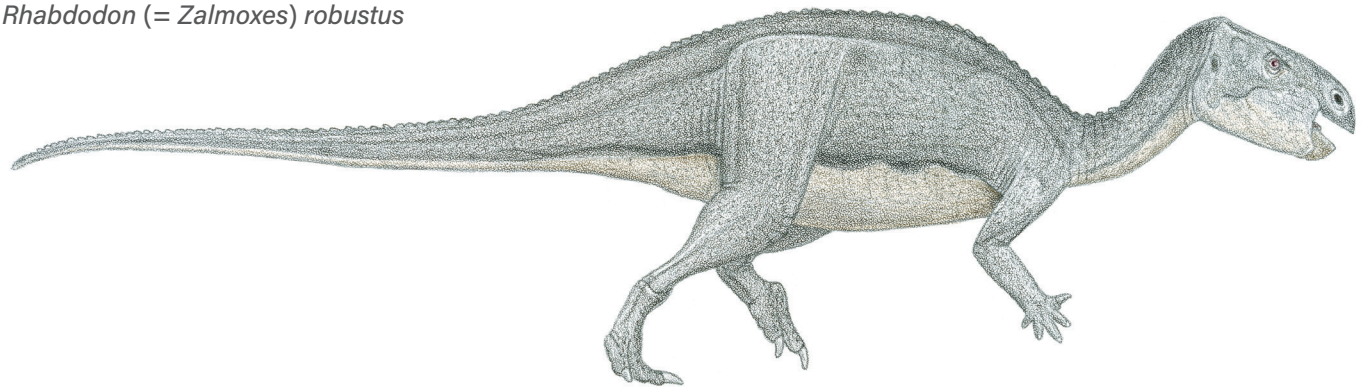
— 4 m (13 ft) TL, 320 kg (700 lb)
FOSSIL REMAINS Minority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Similar to *R. robustus*.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southwestern France, possibly Spain, Austria, Hungary; Grès de Labarre, Marnes Rouges Inférieures, Grès de Saint-Chinian.
HABITAT/S Forested islands.
NOTES Is uncertain whether all the remains from the various formations, including those once placed in *Mochlodon suessi*, belong to this species. Some possible *R. priscus* remains are of 6 m (20 ft) individuals. May be ancestor of *R. robustus*.

Rhabdodon (= *Zalmoxes*) *robustus*

— 2.9 m (9.5 ft) TL, 122 kg (270 lb)
FOSSIL REMAINS Majority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Head fairly deep, subrectangular in side view, crestless, eye shaded by overhanging rim, teeth large.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Romania; Sânpetru.

Rhabdodon (= *Zalmoxes*) *robustus*
(see also next page)

Rhabdodon (= *Zalmoxes*) *robustus*



HABITAT/S Forested islands.
NOTES *Z. shqiperorum* probably adult of this species.

Matheronodon provincialis

— 4 m (13 ft) TL, 300 kg (600 lb)
FOSSIL REMAINS Minority of skull and isolated teeth.
ANATOMICAL CHARACTERISTICS Teeth very enlarged and robust, reduced in number.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southeastern France; Gres de Reptiles.
HABITAT/S Forested islands.
HABITS Probably specialized in consuming tough, highly abrasive fiber vegetation.

— DRYOSAURIDS

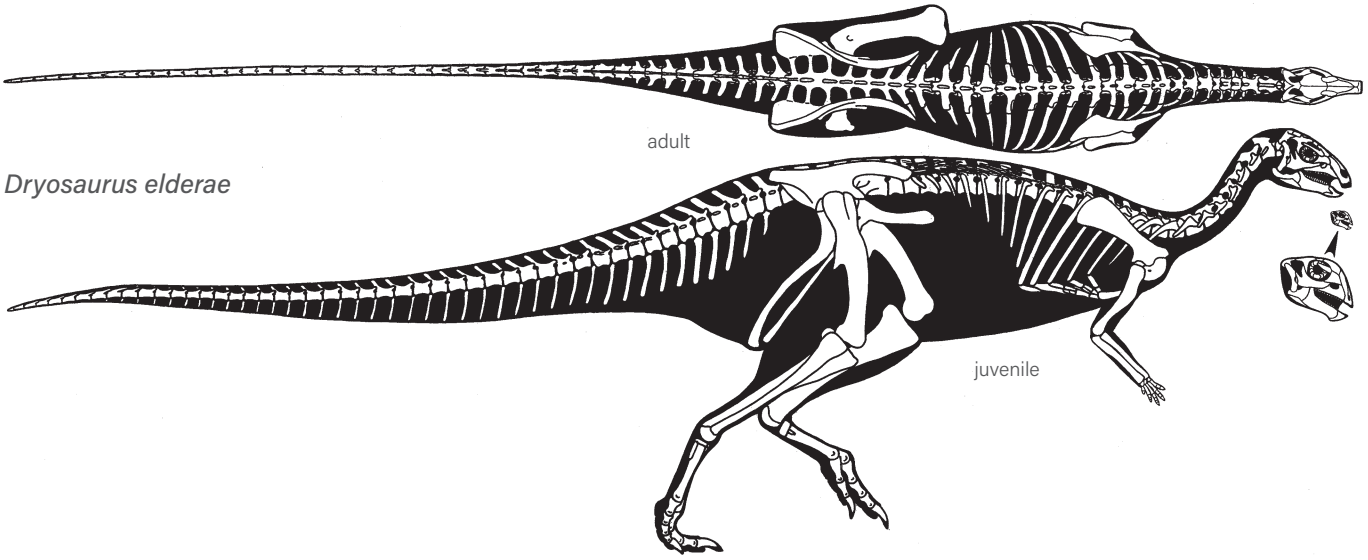
SMALL TO MEDIUM-SIZED IGUANODONTIANS LIMITED TO THE LATE JURASSIC AND EARLY CRETACEOUS OF NORTH AMERICA, EUROPE, AND AFRICA.

ANATOMICAL CHARACTERISTICS Highly uniform. Heads small, subtriangular, beaks small, partly squared off, eyes shaded by overhanging rim. Trunks and hips fairly narrow. Arms short so fully bipedal. Hands broad, five short grasping fingers tipped with very small, blunt claws. Legs fairly gracile, three long toes tipped with blunt claws.
HABITS Low-level browsers. Main defense running.

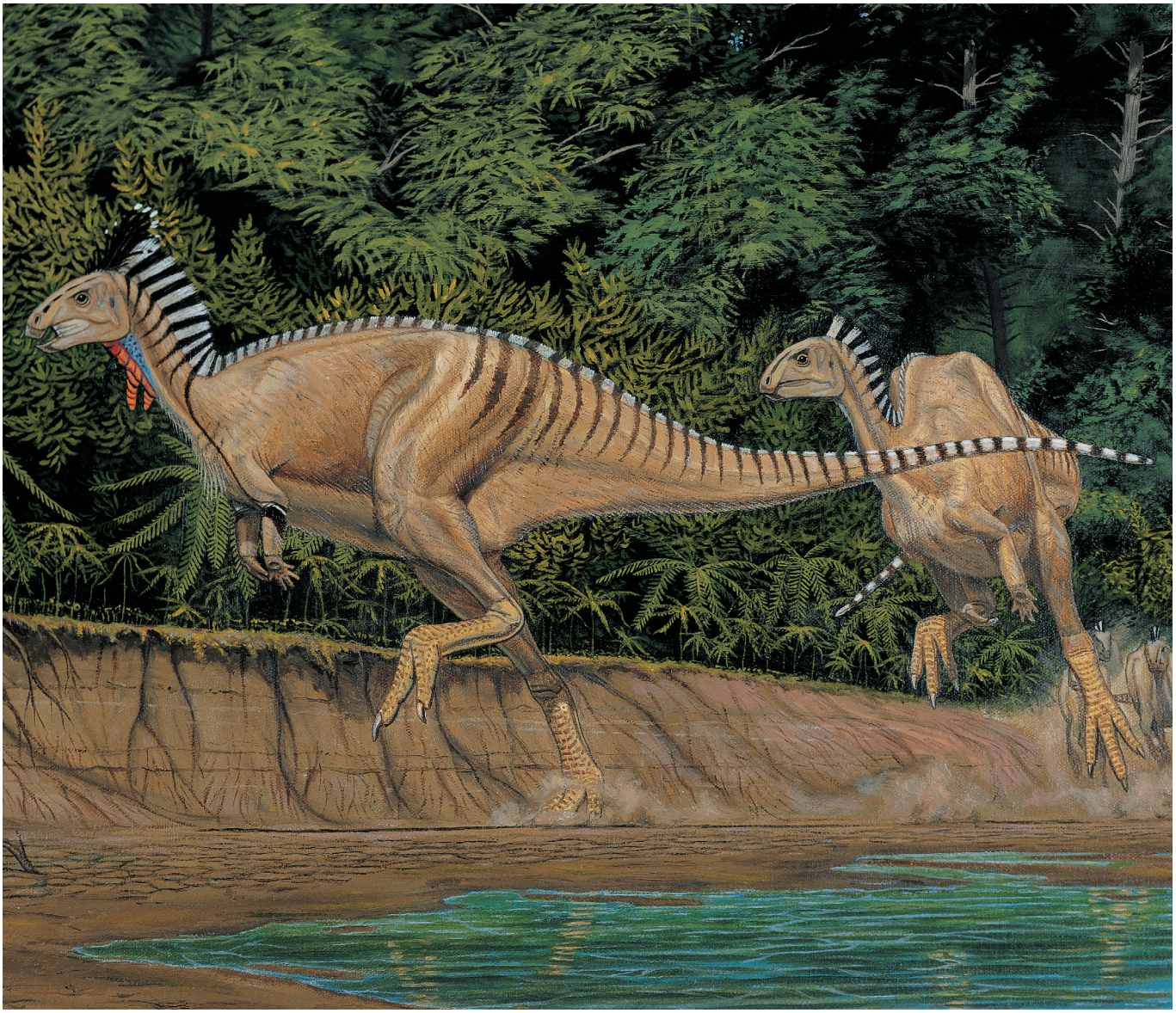
Dryosaurus elderae

— 3 m (10 ft) TL, 100 kg (220 lb)
FOSSIL REMAINS Complete skull and skeleton, other skeletons, nearly completely known.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Utah; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES Once placed in later *D. altus*. It has been suggested that the largest known fossils are not mature, but absence of larger individuals leaves this possibility unsupported.

Dryosaurus elderae



Dryosaurus elderae



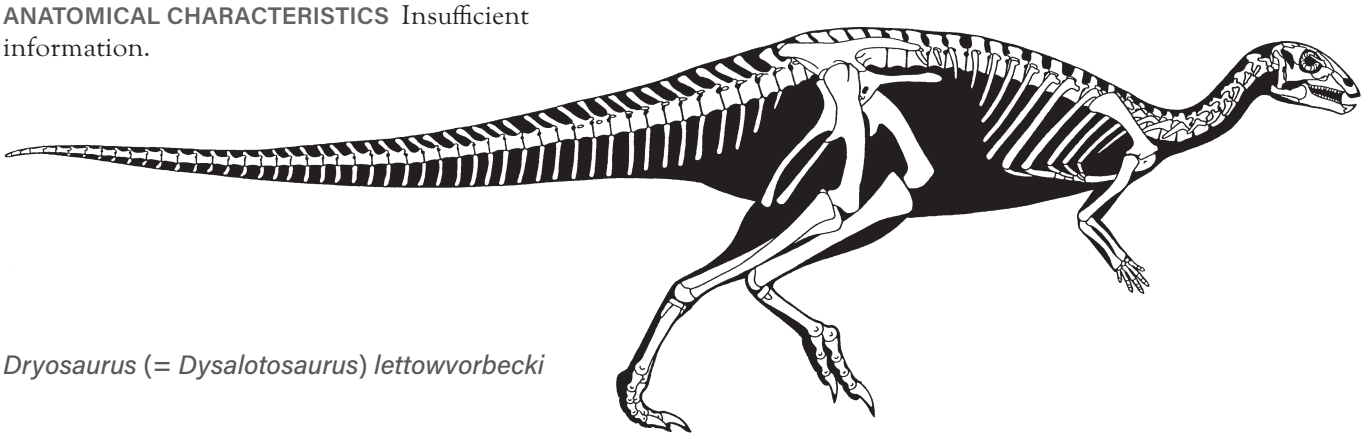
Dryosaurus altus

— 3 m (10 ft) TL, 110 kg (250 lb)
FOSSIL REMAINS Partial skeletons and skeletal parts.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, late middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Wyoming; upper Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

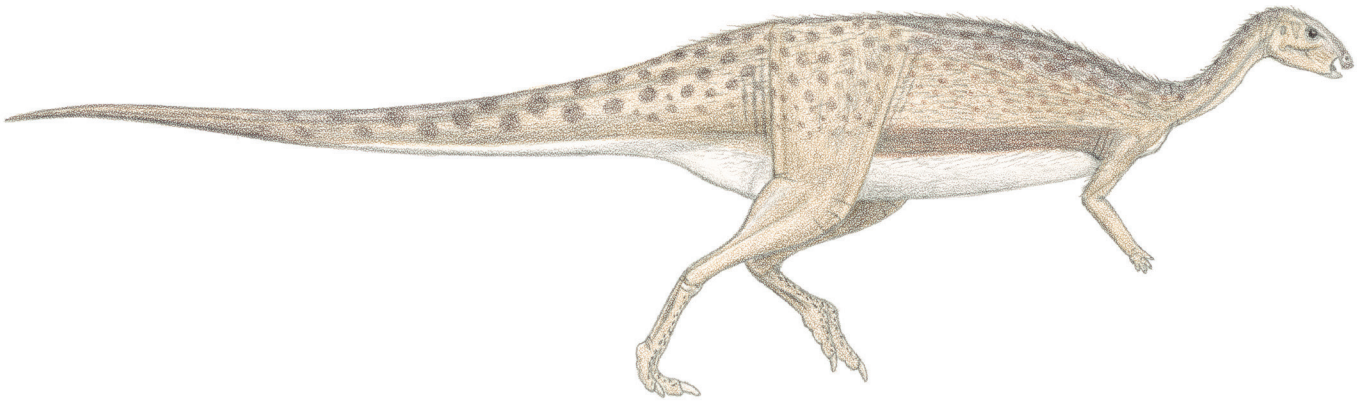
Dryosaurus (= *Dysalotosaurus*) *lettowvorbecki*
— 2.5 m (8 ft) TL, 86 kg (190 lb)
FOSSIL REMAINS A large number of skull and skeletal parts, nearly completely known.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Tanzania; middle Tendaguru.
HABITAT/S Coastal, seasonally dry with heavier vegetation inland.
NOTES Generic separation from very similar *D. altus* is a classic case of oversplitting.

Valdosaurus canaliculatus
— 4 m (13 ft) TL, 400 kg (900 lb)
FOSSIL REMAINS Partial skeleton and other partial remains.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, middle Barremian.
DISTRIBUTION AND FORMATION/S Southern England; upper Wessex.
NOTES Placement of remains from Romania and Niger in this species or genus is highly problematic.

Planicoxa venenica
— 4.5 m (15 ft) TL, 450 kg (1,000 lb)
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, upper Barremian.
DISTRIBUTION AND FORMATION/S Utah; middle Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.



Dryosaurus (= *Dysalotosaurus*) *lettowvorbecki*



— ANKYLOPOLLEXIANS

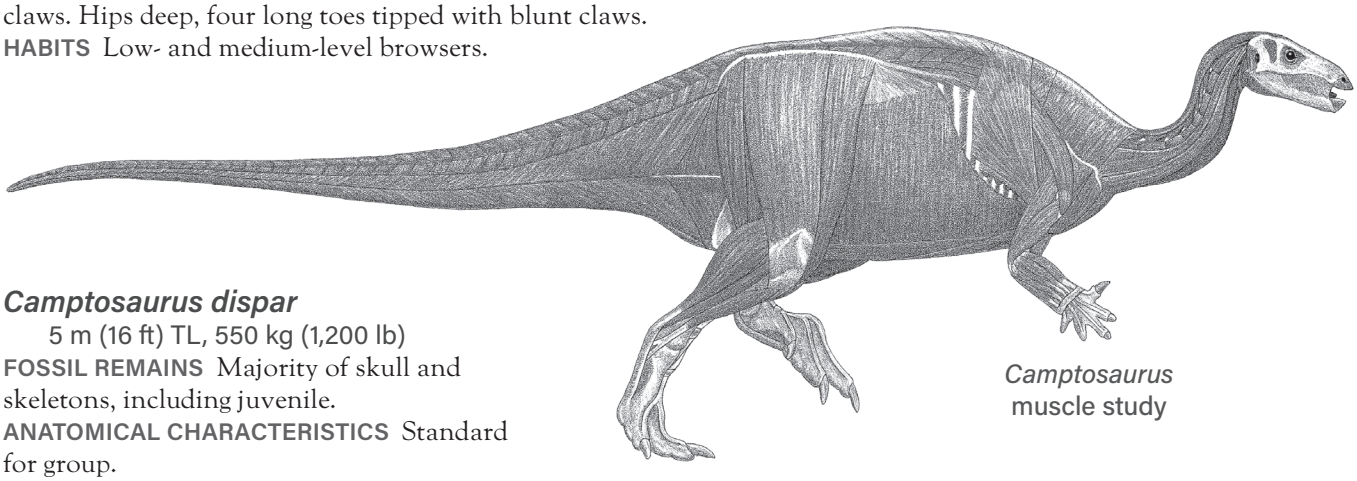
SMALL TO GIGANTIC IGUANODONTIANS FROM THE LATE JURASSIC TO THE END OF THE DINOSAUR ERA, ALL CONTINENTS.

ANATOMICAL CHARACTERISTICS Heads narrow. Strongly bipedal to semiquadrupedal. Thumb claws when present are spikes.
HABITAT/S Variable, from tropics to polar winters, from semiarid to wet.
HABITS Thumb spikes used for competition within the species and for defense against predators.
NOTES At least some ankylopollexians without bony head crests may have had soft-tissue crests.

— CAMPTOSAURIDS

MEDIUM-SIZED TO LARGE IGUANODONTIANS LIMITED TO THE LATE JURASSIC TO EARLY CRETACEOUS OF NORTH AMERICA, EUROPE, AND AUSTRALIA.

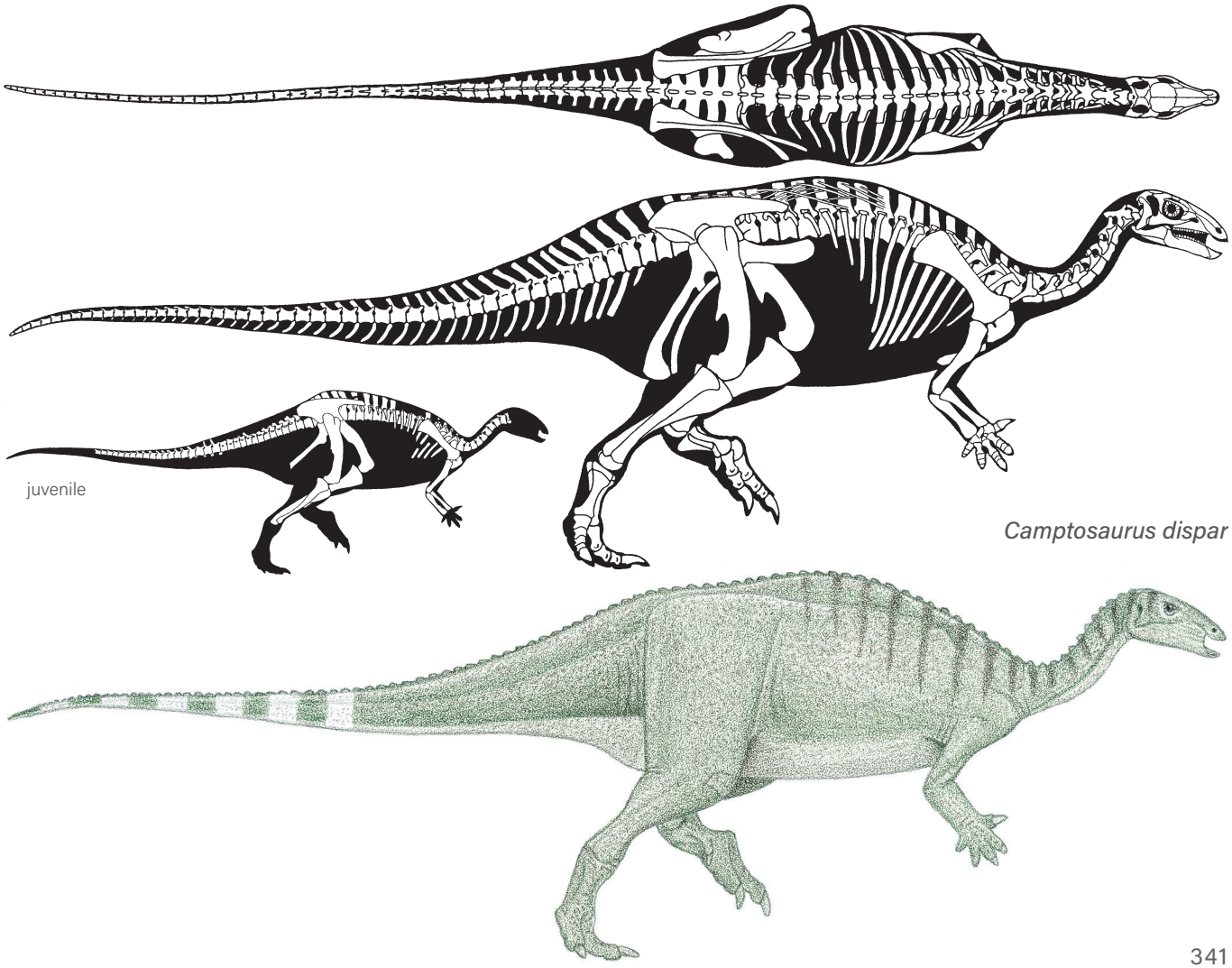
ANATOMICAL CHARACTERISTICS Heads fairly small and subtriangular, beaks narrow, eyes shaded by overhanging rim. Trunks and hips fairly broad. Bipedal except could move quadrupedally at slow speeds. Arms fairly short, so strongly bipedal; hands short, broad, five grasping fingers tipped with small claws. Hips deep, four long toes tipped with blunt claws.
HABITS Low- and medium-level browsers.



Camptosaurus muscle study

Camptosaurus dispar

5 m (16 ft) TL, 550 kg (1,200 lb)
FOSSIL REMAINS Majority of skull and skeletons, including juvenile.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, latest Oxfordian.



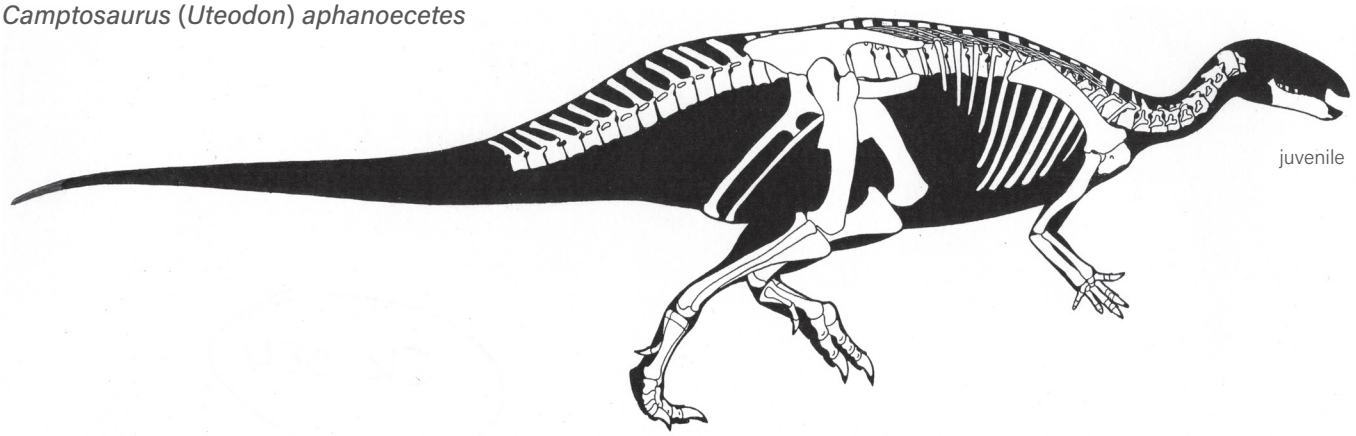
DISTRIBUTION AND FORMATION/S Wyoming; lower Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.

Camptosaurus (Uteodon) aphanoecetes
— Adult size uncertain
FOSSIL REMAINS Majority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, early and/or early middle Kimmeridgian.
DISTRIBUTION AND FORMATION/S Utah; middle Morrison.
HABITAT/S Short wet season, otherwise semiarid with open floodplain prairies and riverine forests.
NOTES May be the direct descendant of *C. dispar*. Remains that belong to this or another species indicate individuals approached 2 tonnes.

Cumnoria (or *Camptosaurus*) *prestwichii*
— Adult size uncertain
FOSSIL REMAINS Minority of skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, Kimmeridgian.
DISTRIBUTION AND FORMATION/S Eastern England; Kimmeridge Clay.
NOTES Juvenile fossil hinders determination of whether this is *Camptosaurus*.

Draconyx loureiroi
— 3.5 m (11 ft) TL, 150 kg (300 lb)
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Standard for group.
AGE Late Jurassic, late Tithonian.
DISTRIBUTION AND FORMATION/S Portugal; upper Lourinhã.
HABITAT/S Large, seasonally dry island with open woodlands.

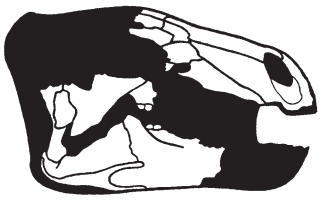
Camptosaurus (*Uteodon*) *aphanoecetes*



— ANKYLOPOLLEXIAN MISCELLANEA

NOTES **The relationships of these ankylopollexians are uncertain.**

Hippodraco scutodens
— 4.5 m (15 ft) TL, 400 kg (900 lb)
FOSSIL REMAINS Partial skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, upper Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.



Theiophytalia kerri

Theiophytalia kerri
— 5 m (16 ft) TL, 500 kg (1,000 lb)
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Snout subrectangular.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Colorado; Purgatoire.
NOTES Until recently this skull was mistakenly thought to be from the much earlier Morrison Formation and was incorrectly used to restore *Camptosaurus* with a deep, subrectangular snout.

Huxleysaurus hollingtoniensis
— 7 m (23 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.

AGE Early Cretaceous, early Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; Wadhurst Clay.
NOTES Originally placed in *Iguanodon*, whose type species has been moved to a much later date; placement in *Hypselospinus fittoni* has not been substantiated.

— IGUANODONTOIDS

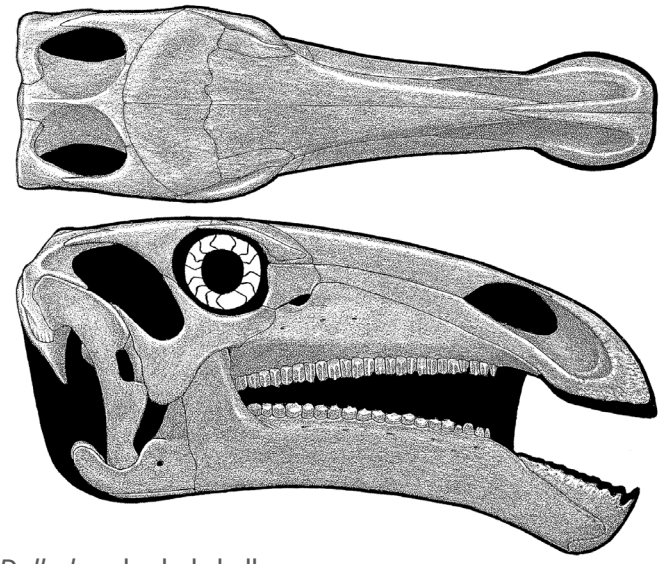
MEDIUM-SIZED TO GIGANTIC ANKYLOPOLLEXIANS OF THE CRETACEOUS OF THE AMERICAS, EURASIA, AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads not deep, snouts elongated, nasal openings enlarged, upper beaks projecting well below level of upper tooth row, lower beak edges serrated, vertical coronoid projections on lower jaws very well developed, grinding tooth batteries well developed. Heads strongly flexed on necks. Necks longer and more slender and flexible than in other ornithopods. Trunk and tail vertebrae stiffened by a dense crisscross lattice of ossified tendons, spines at least fairly tall. Medium-length tails deep and flattened from side to side along most of length. Arm length from moderately long to long, so strongly bipedal to semiquadrupedal. Central three fingers short, inflexible, and hooved, outer fingers long, flexible, and divergent, providing limited grasping ability. Three toes shortened, inflexible, and hooved.
HABITAT/S Variable, from tropics to polar winters, from seasonally arid to well-watered forests.
HABITS Medium- and low-level browsers and grazers. Tails too stiff to be used as a sculling organ when swimming.
NOTES The oversized cattle of the Cretaceous, and the most common large herbivores of that period.

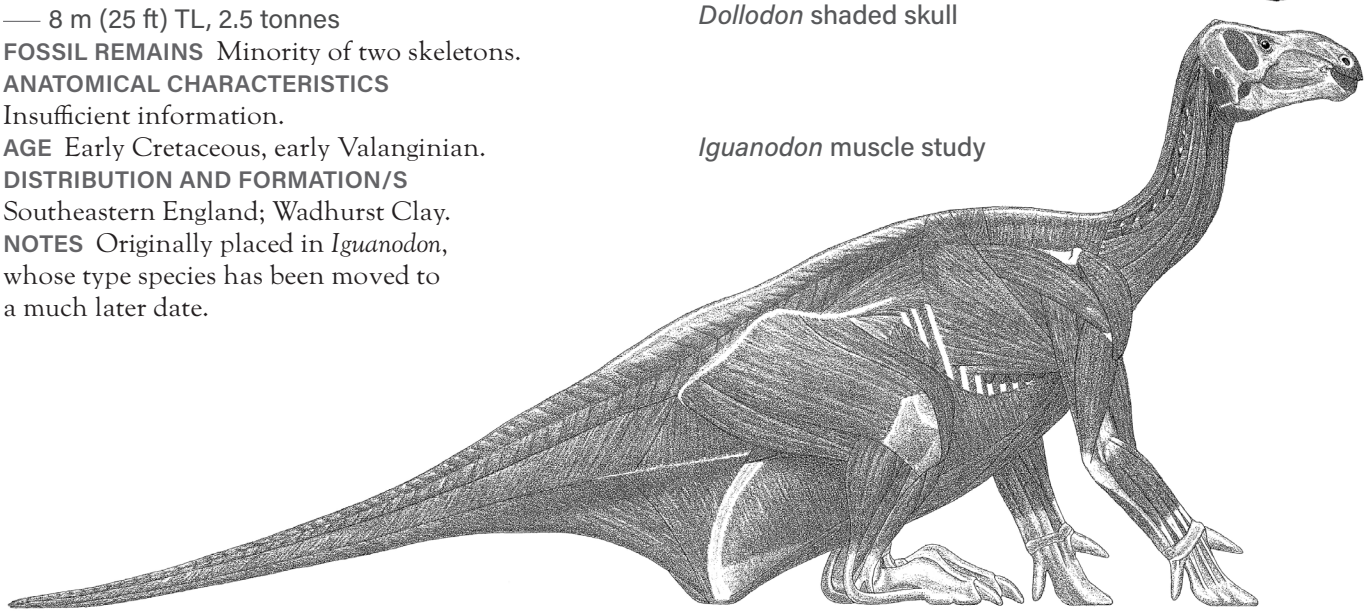
— IGUANODONTS

MEDIUM-SIZED TO VERY LARGE IGUANODONTOIDS LIMITED TO THE EARLY CRETACEOUS OF NORTH AMERICA, EURASIA, AND AFRICA.

ANATOMICAL CHARACTERISTICS Fairly uniform. Heads fairly shallow, snouts long, eyes usually shaded by overhanging rim. Thumb spikes anchored on heavily built wrist bones.
NOTES Iguanodonts are basal iguanodontoids excluding hadrosauromorphs. Relationships within the group are not well understood; ultimately splittable into a number of subdivisions. Absence from Australia and Antarctica may reflect lack of sufficient sampling.



Dollodon shaded skull

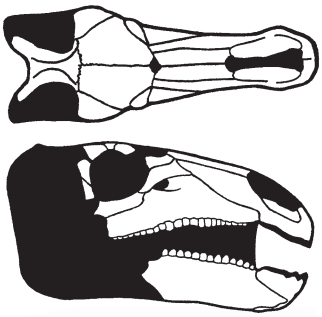


Iguanodon muscle study

Barilium dawsoni

— 8 m (25 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of two skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; Wadhurst Clay.
NOTES Originally placed in *Iguanodon*, whose type species has been moved to a much later date.

Dakotadon lakotaensis
— 6 m (20 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull, small portion of skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular, beak narrow and rounded.
AGE Early Cretaceous, probably Barremian.
DISTRIBUTION AND FORMATION/S South Dakota; Lakota.
HABITS Middle- and low-level browser.
NOTES Originally placed in European *Iguanodon*, whose type species has been moved to a much later date.



Dakotadon lakotaensis

Iguanacolossus fortis
— 9 m (30 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Heavily constructed.
AGE Early Cretaceous, late Berriasian.
DISTRIBUTION AND FORMATION/S Utah; lowermost Cedar Mountain.

Lanzhousaurus magnidens
— 10 m (35 ft) TL, 6 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Heavily constructed. Lower jaw fairly deep, teeth extremely large. Modest shoulder withers support nuchal ligaments to neck and head.
AGE Early Cretaceous.
DISTRIBUTION AND FORMATION/S Central China; Hekou Group.
HABITS Middle- and low-level browser, able to consume coarse vegetation.
NOTES Had largest known teeth of any herbivorous dinosaur.

Lurdusaurus arenatus
— 7 m (23 ft) TL, 2.5 tonnes
FOSSIL REMAINS Small portion of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Arm massively constructed, hand short and broad, thumb spike enormous.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Niger; upper Elrhaz.
HABITAT/S Coastal river delta.
HABITS Middle- and low-level browser.

Darwinsaurus evolutionis
— 6.5 m (21 ft) TL, 1 tonne
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Lower jaw shallow, very long gap between beak and short main tooth rows. Arm massively constructed, upper hand long and narrow, thumb spike enormous.
AGE Early Cretaceous, early Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; Wadhurst Clay.
NOTES Originally placed in *Iguanodon*, whose type species has been moved to a much later date; placement in *Hypselospinus fittoni* has not been substantiated.

Brighstoneus simmondsi
— 6 m (20 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head elongated and low, low crest over nostrils, lower jaw shallow.
AGE Early Cretaceous, early Barremian.
DISTRIBUTION AND FORMATION/S Southeastern England; lower Wessex.

Brighstoneus simmondsi

Sellacoxa pauli
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; lower Wadhurst Clay.
NOTES Placement in *Hypselospinus fittoni* has not been substantiated.

Hypselospinus fittoni
— 7 m (23 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of several skulls.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Cretaceous, early Valanginian.
DISTRIBUTION AND FORMATION/S Southeastern England; Wadhurst Clay.

NOTES Originally placed in *Iguanodon*, whose type species has been moved to a much later date.

Unnamed genus? *galvensis*

— Adult size uncertain

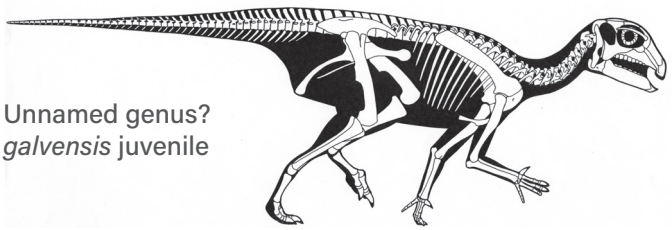
FOSSIL REMAINS Numerous partial skulls and skeletons of subadults and juveniles.

ANATOMICAL CHARACTERISTICS Heavily built.

AGE Early Cretaceous, early Barremian.

DISTRIBUTION AND FORMATION/S Spain; Camarillas.

NOTES Placement in markedly later *Iguanodon* problematic. May be an ancestor of *I. bernissartensis*.



Unnamed genus? *galvensis* juvenile

Iguanodon bernissartensis

— 8 m (26 ft) TL, 3.3 tonnes

FOSSIL REMAINS Over two dozen complete skulls and skeletons, completely known.

ANATOMICAL CHARACTERISTICS Heavily constructed. Head subrectangular, beak narrow and rounded, lower jaw fairly deep. Arm long, so semiquadrupedal; hand and spike very large, upper hand long and fairly narrow. Foot large.

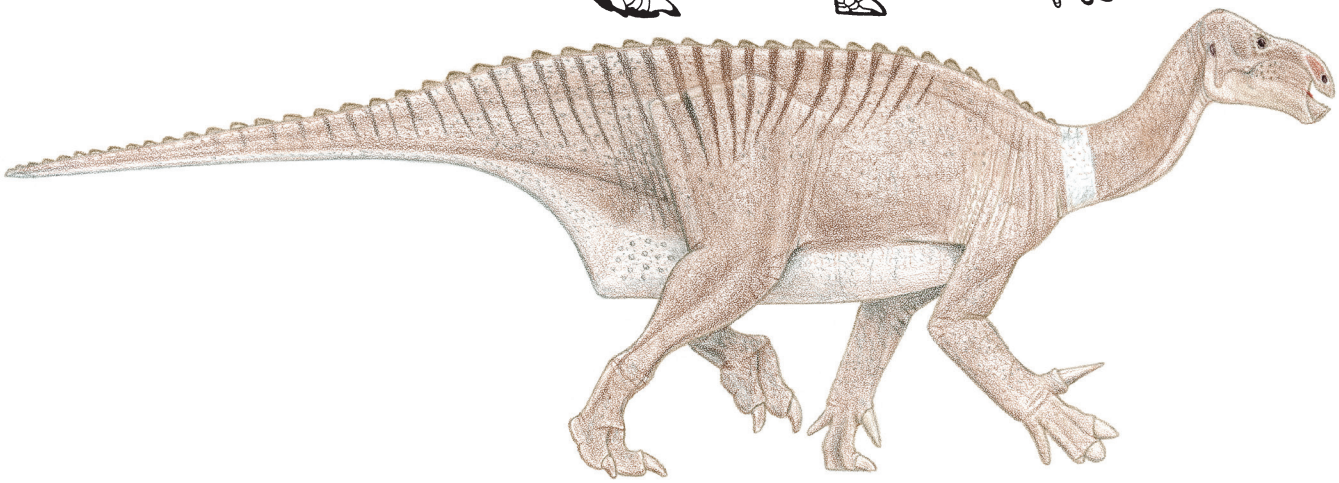
AGE Early Cretaceous, probably late Barremian, possibly earliest Aptian.

DISTRIBUTION AND FORMATION/S Belgium; upper Sainte-Barbe Clays.

HABITS Middle- and low-level browser.

NOTES The classic iguanodont. Over the years *Iguanodon* became a taxonomic grab bag into which a large number of remains from many places and times were placed. In accord with a decision of the committee that handles such issues, this is now the set of remains that is labeled *Iguanodon*. The original English teeth the genus was based on are much older, from the Valanginian, but are not distinctive. Other fossils that probably belong to *Iguanodon*

Iguanodon bernissartensis



ABOVE: *Iguanodon bernissartensis*

Dollodon bampingi

and may or may not belong to this species are known from Germany and England, not common in the latter country. Found in ancient sinkhole fill of uncertain age.

Dollodon bampingi

— 6.5 m (21 ft) TL, 1.1 tonnes

FOSSIL REMAINS Complete skull and skeleton.

ANATOMICAL CHARACTERISTICS Head shallow, subrectangular, snout very long, beak narrow and rounded, significant gap between beak and tooth rows. Tall vertebral spines over trunk, hips, and tail form a shallow sail. Arm fairly long, so semiquadrupedal; upper hand long and narrow, thumb claw small.

AGE Early Cretaceous, probably late Barremian, possibly earliest Aptian.

DISTRIBUTION AND FORMATION/S Belgium; upper Sainte-Barbe Clays.

HABITS Middle- and low-level browser.

NOTES Found in ancient sinkhole fill. Has been confused with distinct and probably later *Mantellisaurus*.

Mantellisaurus atherfieldensis

— Adult size uncertain

FOSSIL REMAINS Nearly complete skull and majority of skeleton, numerous bones.

ANATOMICAL CHARACTERISTICS Snout long, beak narrow and rounded. Bipedal except could move quadrupedally at slow speeds. Arm fairly short, so largely bipedal; upper hand long and narrow, thumb claw small. Toes longer than in other iguanodonts.

AGE Early Cretaceous, earliest Aptian.

DISTRIBUTION AND FORMATION/S Southern England; upper Vectis.

HABITS Middle- and low-level browser.

NOTES Incorrectly placed in *Iguanodon*; placement of many incomplete English remains in this taxon is problematic. May be ancestor of *Mantellodon carpenteri*.

Mantellodon carpenteri

— Adult size uncertain

FOSSIL REMAINS Partial skeleton.

ANATOMICAL CHARACTERISTICS Insufficient information.

AGE Early Cretaceous, early Aptian.

DISTRIBUTION AND FORMATION/S Southeastern England; lower lower Greensand.

NOTES Incorrectly placed in *Iguanodon*; placement in probably earlier *Mantellisaurus atherfieldensis* probably incorrect.

Proa valdearinnoensis

— 5.5 m (18 ft) TL, 1 tonne

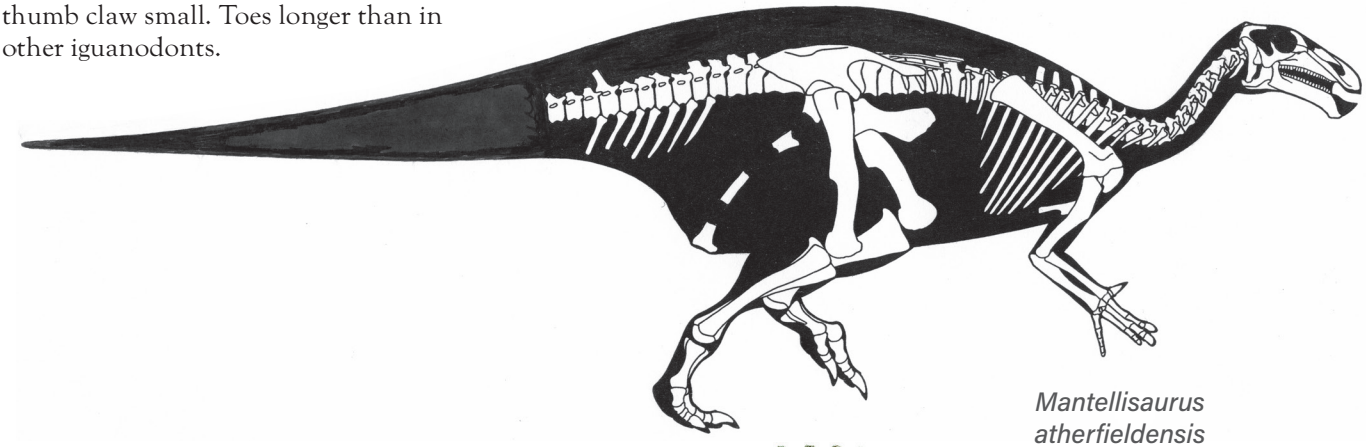
FOSSIL REMAINS Partial skulls and skeletons.

ANATOMICAL CHARACTERISTICS Robustly built. Beak narrow and rounded.

AGE Early Cretaceous, early Albian.

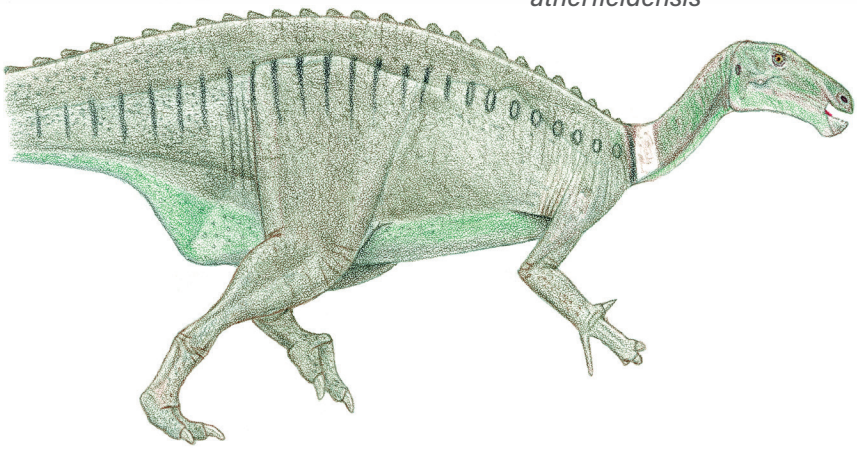
DISTRIBUTION AND FORMATION/S Spain; Escucha.

HABITS Middle- and low-level browser.



Mantellisaurus atherfieldensis

Proa valdearinnoensis



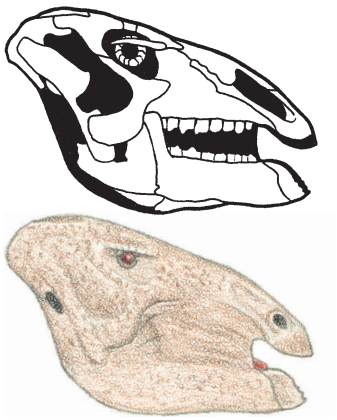
Xuwulong yueluni
— 5 m (16 ft) TL, 650 kg (1,400 lb)
FOSSIL REMAINS Complete skull and majority of skeleton.
ANATOMICAL CHARACTERISTICS Head subrectangular, beak small. Front half of tail very deep.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Central China; Xinminbao Group.
NOTES Absence of limbs precludes skeletal restoration.

Equijubus normani
— 7 m (23 ft) TL, 2.5 tonnes
FOSSIL REMAINS Complete skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Head subtriangular, beak narrow and rounded, eyes not shaded by overhanging rim, long gap between beak and main tooth rows, incipient third tooth in each position.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Central China; middle Xinminbao Group.
HABITS Middle- and low-level browser.

Bolong yixianensis
— Adult size uncertain
FOSSIL REMAINS Two largely complete juvenile fossils.
ANATOMICAL CHARACTERISTICS Robustly built. Beak rounded. Tail not large. Arm and hand short, so largely bipedal; thumb claw small.
AGE Early Cretaceous, latest Barremian and/or earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; middle Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Middle- and low-level browser.

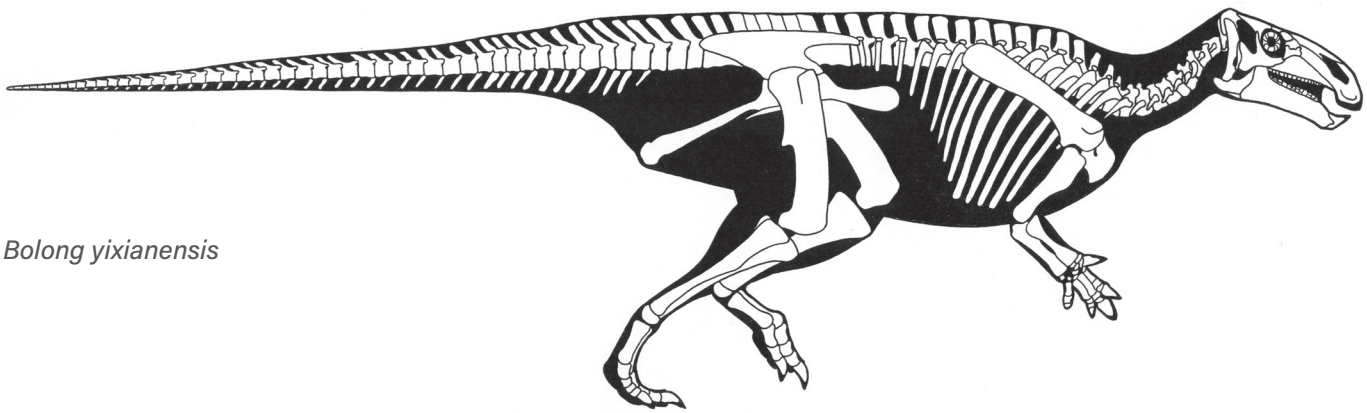
Jinzhousaurus yangi
— 5 m (16 ft) TL, 700 kg (1,500 lb)
FOSSIL REMAINS Complete skull and skeleton.
ANATOMICAL CHARACTERISTICS Robustly built. Beak large, narrow, and rounded. Tail not large. Arm and hand short, so largely bipedal; thumb claw small.
AGE Early Cretaceous, earliest Aptian.
DISTRIBUTION AND FORMATION/S Northeastern China; upper Yixian.
HABITAT/S Well-watered volcanic highland forest-and-lake district, winters chilly with snow.
HABITS Middle- and low-level browser.

Fukuisaurus tetoriensis
— 4.5 m (15 ft) TL, 400 kg (900 lb)
FOSSIL REMAINS Majority of skull.

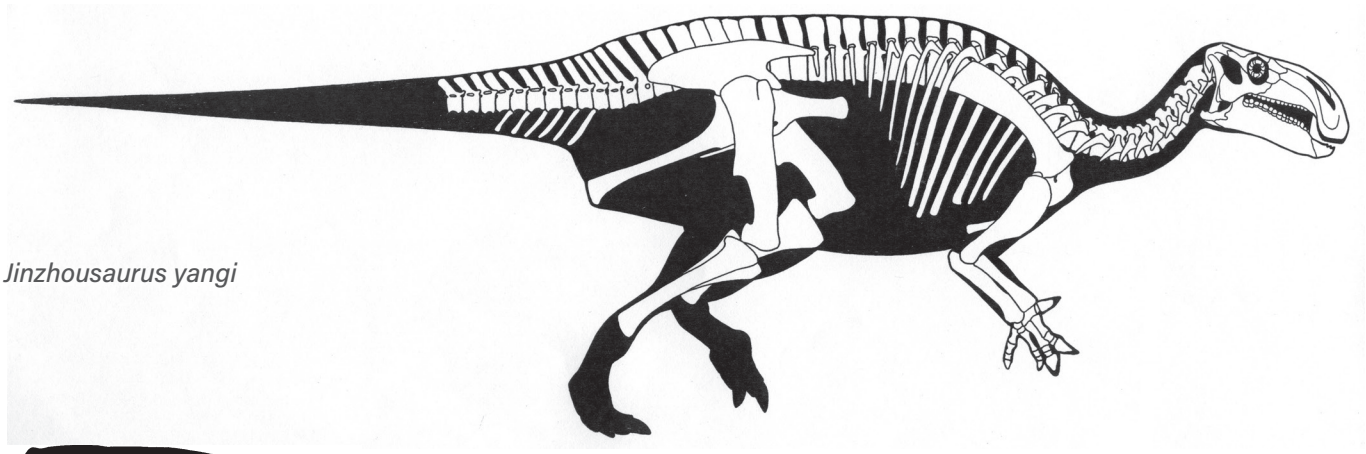


Xuwulong yueluni

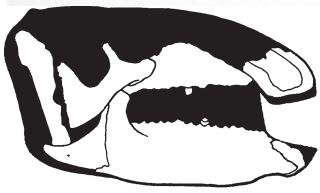
Equijubus normani



Bolong yixianensis



Jinzhousaurus yangi



Fukuisaurus tetoriensis

ANATOMICAL CHARACTERISTICS Head short and fairly deep.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Central Japan; Kitadani.

Choyrodon barsboldi

— Adult size uncertain
FOSSIL REMAINS Three skulls and skeletal remains.
ANATOMICAL CHARACTERISTICS Snout deepened into an arched crest, beak rounded.
AGE Early Cretaceous, middle and/or late Albian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Khuren Dukh.
HABITS Middle- and low-level browser.
NOTES Crest probably became more prominent with maturity.

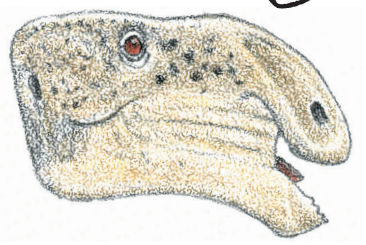
Altirhinus kurzanovi

— 6.5 m (21 ft) TL, 1.1 tonne
FOSSIL REMAINS Nearly complete and partial skulls, minority of skeletons.
ANATOMICAL CHARACTERISTICS Snout deepened into a very prominent arched crest, beak narrow and rounded, incipient third tooth in each position. Upper hand long and narrow.
AGE Early Cretaceous, Aptian or Albian.
DISTRIBUTION AND FORMATION/S Mongolia; Huhteeg Svita.
HABITS Middle- and low-level browser.

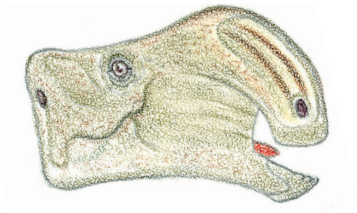
Ouranosaurus nigeriensis

— 8.3 m (27 ft) TL, 2.3 tonnes
FOSSIL REMAINS Complete skull and majority of two skeletons.

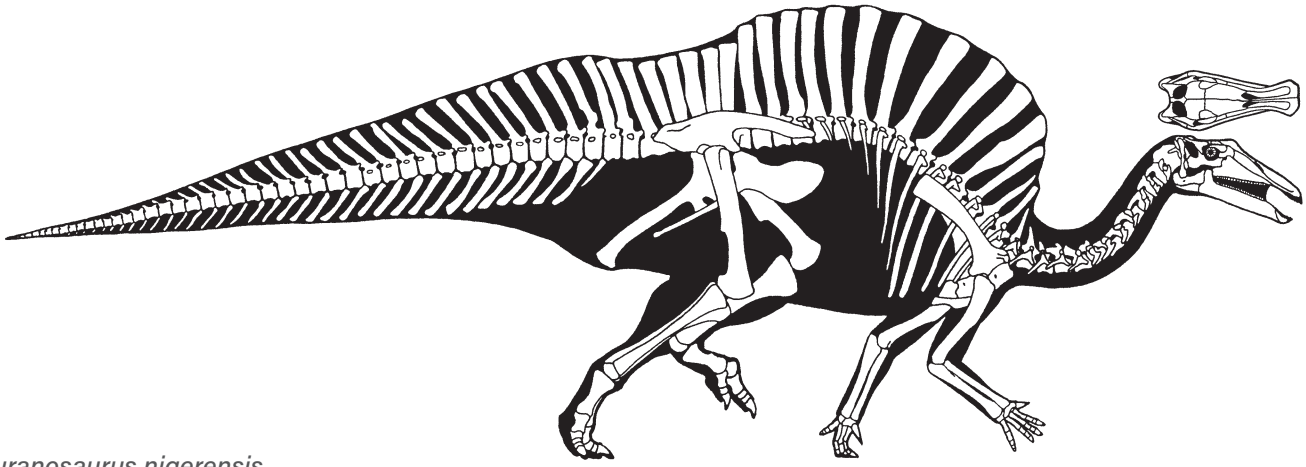
Choyrodon barsboldi



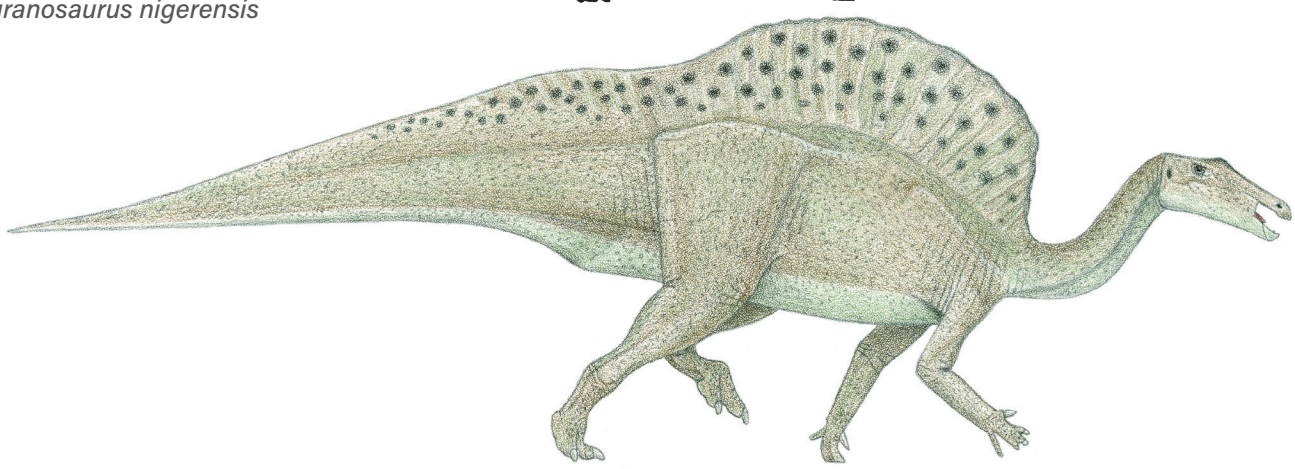
Altirhinus kurzanovi

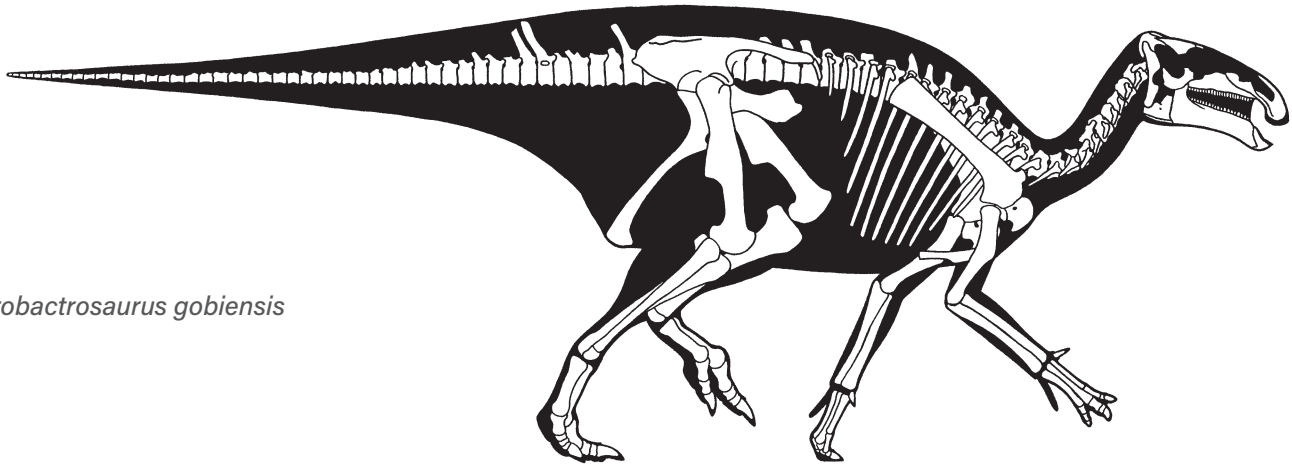


ANATOMICAL CHARACTERISTICS Head shallow, subtriangular, snout very long, low midline crest on top of middle of head, beak broad and partly squared off, very long gap between beak and tooth rows. Very tall vertebral spines over trunk, hips, and tail forming very tall finback sail. Arm fairly long, so semiquadrupedal; upper hand short and broad, thumb claw small.
AGE Early Cretaceous, late Aptian.
DISTRIBUTION AND FORMATION/S Niger; upper Elrhaz.
HABITAT/S Coastal river delta.

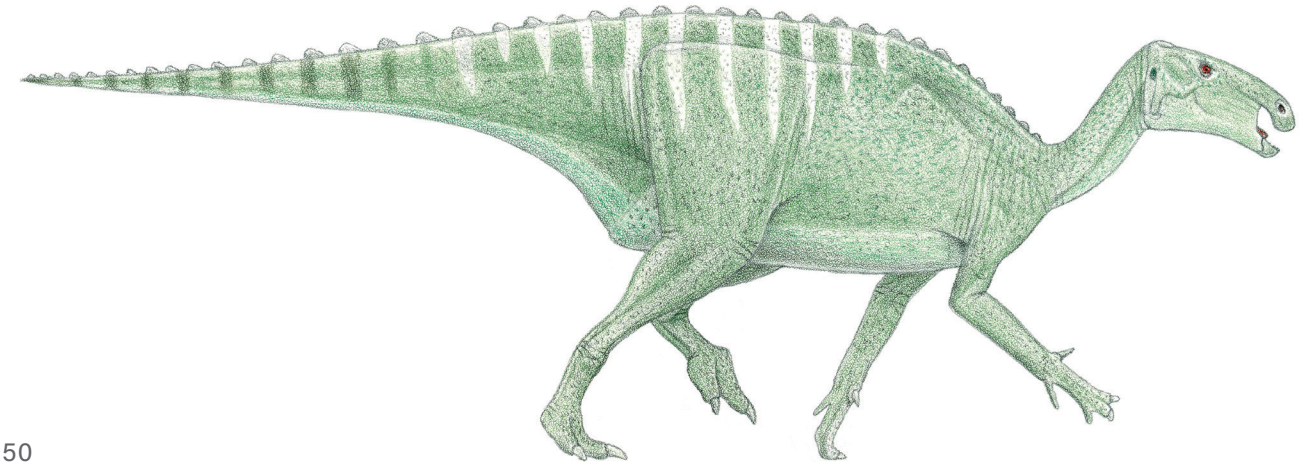


Ouranosaurus nigerensis





Probactrosaurus gobiensis



HABITS Square muzzle at end of long snout is adaptation for reaching down to and mowing ground cover; also able to browse at low and medium levels.

Probactrosaurus gobiensis

— 5.5 m (18 ft) TL, 1.1 tonnes
FOSSIL REMAINS Majority of several skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head subrectangular, beak narrow and rounded, significant gap between beak and tooth rows, incipient third tooth in each position. Arm long, so semiquadrupedal; upper hand long and narrow, thumb claw small.
AGE Early Cretaceous, Albian.
DISTRIBUTION AND FORMATION/S Northern China; Dashuigou.
HABITS Middle- and low-level browser.
NOTES Probably includes *P. alashanicus*.

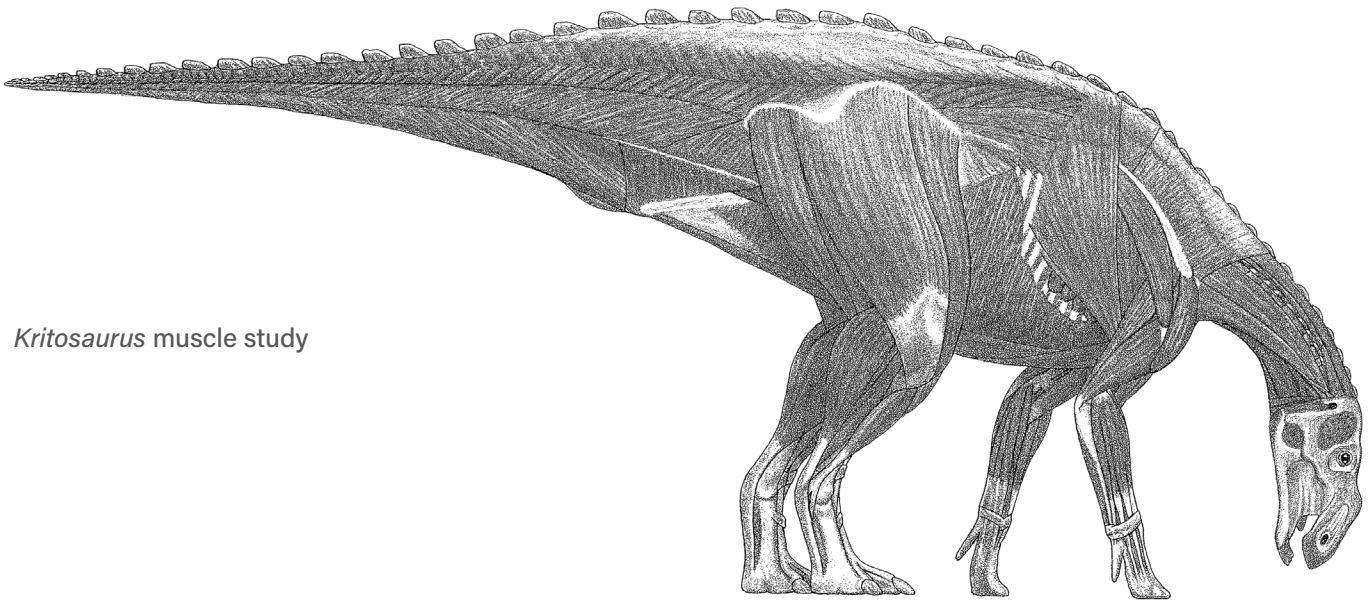
Cedrorestes crichtoni

— Adult size uncertain
FOSSIL REMAINS Minority of skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Early Early Cretaceous, late Valanginian.
DISTRIBUTION AND FORMATION/S Utah; lower Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
NOTES Relationships problematic; if a hadrosaurid, is only one known from the Early Cretaceous.

— HADROSAUROMORPHS

LARGE TO GIGANTIC IGUANODONTOIDS LIMITED TO THE LATE CRETACEOUS OF THE AMERICAS, EURASIA, AND ANTARCTICA.

ANATOMICAL CHARACTERISTICS Uniform, especially noncranial skeletons. Eyes usually not shaded by overhanging rim, diastema gap between beak and dental batteries, at least three teeth in each position forming highly developed grinding pavement including hundreds of teeth. Downcurved front trunk vertebral series supports deep nuchal ligaments to neck and head and lowers shoulders; arms also moderately long, so semiquadrupedal; wrist bones reduced, upper hand elongated and narrow, thumbs lost, leaving at most four fingers. Vertical wrinkles in shoulder region in at least some species.
HABITS Main defense running, using gracile arms to improve speed and turning ability, also kicking with legs. One to two dozen eggs deposited in pit nest, covered by mound of soil.

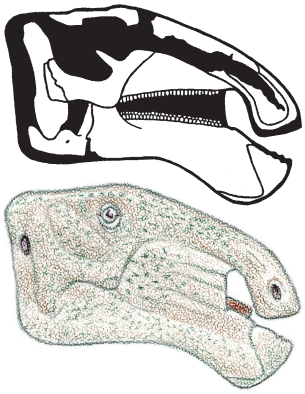


Kritosaurus muscle study

— BASO-HADROSAURS

LARGE HADROSAURS OF THE LATE CRETACEOUS OF THE AMERICAS AND EURASIA.

ANATOMICAL CHARACTERISTICS Uniform. Heads fairly shallow, snouts long, beaks narrow to fairly broad, nasal openings large, bony crests absent, gaps between beaks and tooth rows not long.



Protohadros byrdi

Protohadros byrdi
— Adult size uncertain
FOSSIL REMAINS Majority of skull and minority of skeleton.
ANATOMICAL CHARACTERISTICS Upper beak fairly broad, rounded, projects strongly downward, front of lower jaw deep and curves strongly downward.
AGE Late Cretaceous, middle Cenomanian.
DISTRIBUTION AND FORMATION/S Texas; Woodbine.
HABITAT/S Coastal river delta.
HABITS May have been more prone to feeding on aquatic plants than other iguanodontoids.

Tanius sinensis
— 7 m (23 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of several skulls and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Eastern China; Jiangjunding.

Shuangmiaosaurus gilmorei
— 7.5 m (25 ft) TL, 2.5 tonnes
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Northeastern China; Sunjiawan.

Eolambia caroljonesa

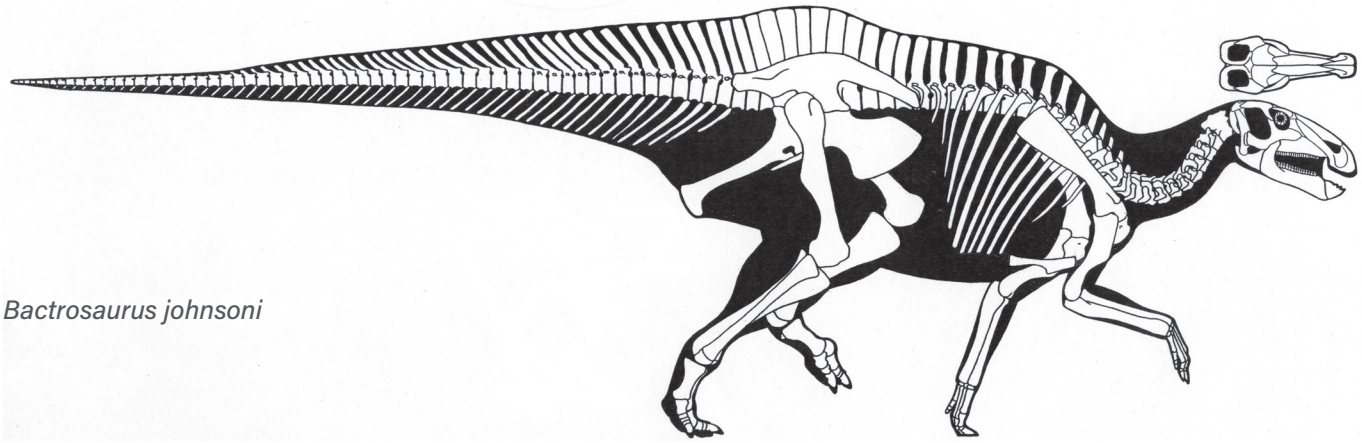
Eolambia caroljonesa
— 6 m (20 ft) TL, 1 tonne
FOSSIL REMAINS Majority of skull and partial skeletons, juvenile to adult.
ANATOMICAL CHARACTERISTICS Beak fairly broad, partly squared off.
AGE Late Cretaceous, early Cenomanian.
DISTRIBUTION AND FORMATION/S Utah; uppermost Cedar Mountain.
HABITAT/S Short wet season, otherwise semiarid with floodplain prairies, open woodlands, and riverine forests.
HABITS Middle- and low-level browser and grazer.

Levnesovia transoxiana
— Adult size uncertain
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle or late Turonian.
DISTRIBUTION AND FORMATION/S Uzbekistan; Bissekty.
HABITAT/S Coastal.

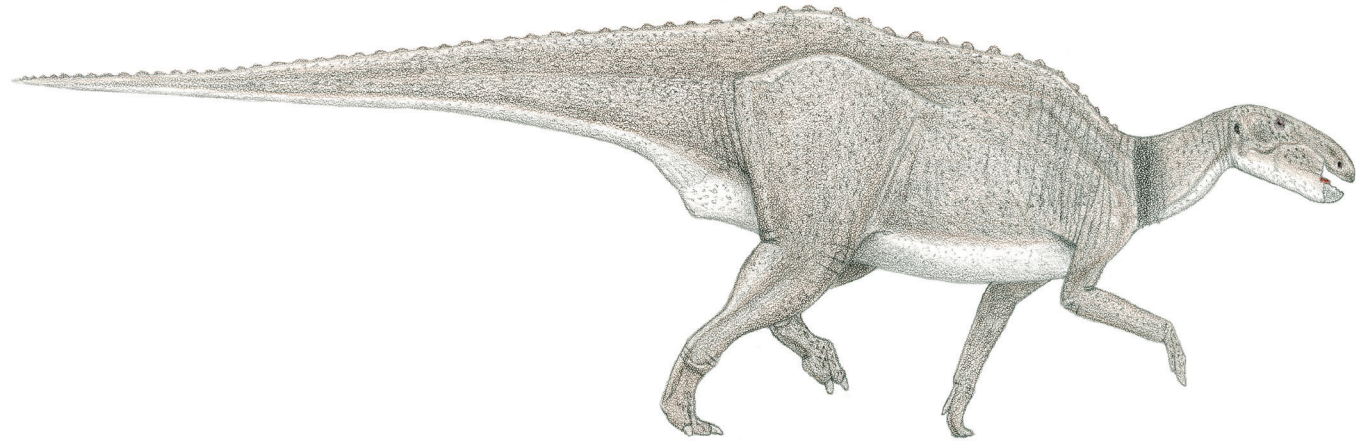
Bactrosaurus johnsoni
— 6.2 m (20 ft) TL, 1.2 tonnes
FOSSIL REMAINS Majority of skulls and skeletons.
ANATOMICAL CHARACTERISTICS Beak narrow, rounded.
AGE Late Cretaceous, probably Campanian.
DISTRIBUTION AND FORMATION/S Northern China; Iren Dabasu.
HABITAT/S Seasonally wet-dry woodlands.
HABITS Middle- and low-level browser.
NOTES Probably includes *Gilmoreosaurus mongoliensis*.

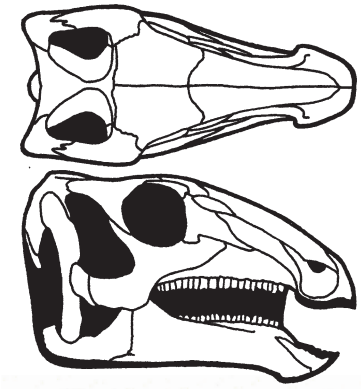
Gobihadros mongoliensis
— Adult size uncertain
FOSSIL REMAINS Two skulls and a skeleton, juveniles.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Cenomanian or Santonian.
DISTRIBUTION AND FORMATION/S Northern China; Baynshiree.
NOTES Immaturity of fossils hinders analysis.

Telmatosaurus transylvanicus
— 5 m (16 ft) TL, 600 kg (1,200 lb)
FOSSIL REMAINS A number of partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Beak narrow, rounded.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Romania; Sânpetru.
HABITAT/S Forested island.
HABITS Middle- and low-level browser.
NOTES Small size of most individuals presumed to represent island dwarfism, but some researchers cite larger fossils and higher estimate of size of island as evidence otherwise.

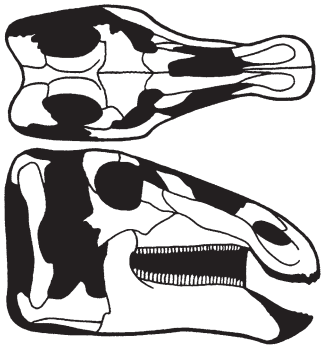


Bactrosaurus johnsoni





Gobihadros mongoliensis



Telmatosaurus transylvanicus

Lophorhothon atopus

— Adult size uncertain

FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Shallow transverse crest over orbits.
AGE Late Cretaceous, latest Santonian.
DISTRIBUTION AND FORMATION/S Alabama; lower Mooreville Chalk.
HABITAT/S Found as drift in nearshore marine sediments.
NOTES A fossil from the earliest Campanian may be later taxon.

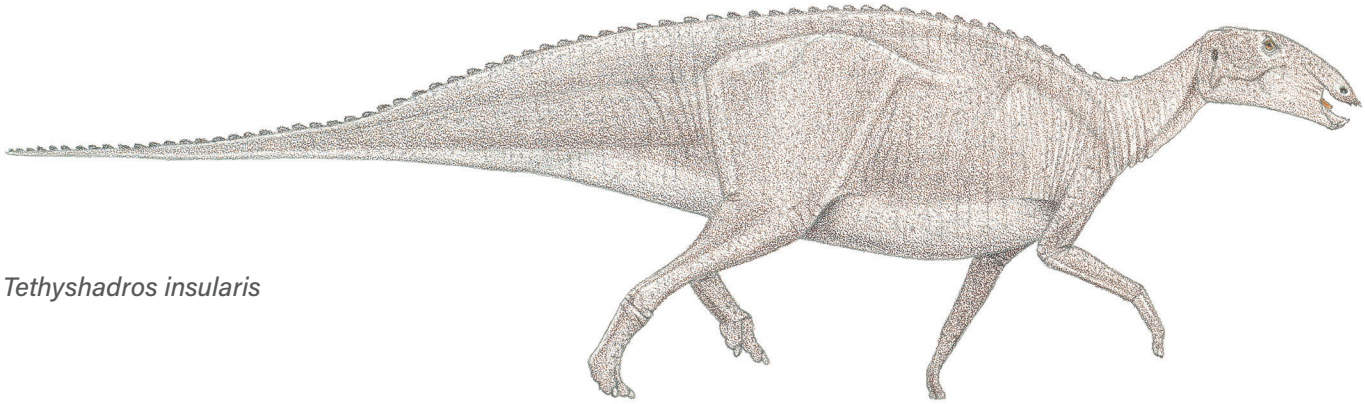
Claosaurus agilis

— Adult size uncertain

FOSSIL REMAINS Minority of skull and partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Late Cretaceous.
DISTRIBUTION AND FORMATION/S Kansas; Niobrara.
NOTES Found as drift in nearshore marine sediments.

Huehuecanauhtlus tiquichensis
— 6 m (20 ft) TL, 1 tonne
FOSSIL REMAINS A number of partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Beak narrow, rounded.
AGE Late Cretaceous, Santonian.
DISTRIBUTION AND FORMATION/S Central Mexico; unnamed formation.

Tethyshadros insularis
— 4.8 m (13 ft) TL, 500 kg (1,100 lb)
FOSSIL REMAINS Nearly complete skull and skeleton, some additional remains.
ANATOMICAL CHARACTERISTICS Upper beak projecting forward, beak serrations well developed, eyes shaded by overhanging rim. Most of tail slender. Only three fingers. Pelvis elongated backward, shifting large portion of gut behind legs. Limbs short relative to mass, lower leg elongated, toes very short.
AGE Late Cretaceous, late Campanian or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Italy; Liburnian.
HABITAT/S A large island.
HABITS Although the limbs are the most speed adapted among hadrosaurs yet known, their shortness is contradictory to very high speeds.
NOTES The smallest known hadrosaur, probably an example of island dwarfing. *Tethyshadros* skeleton is the most distinctive among hadrosaurs yet found.



Tethyshadros insularis

— HADROSAURIDS

LARGE TO GIGANTIC HADROSAURS LIMITED TO THE LATE CRETACEOUS OF THE NORTHERN HEMISPHERE.

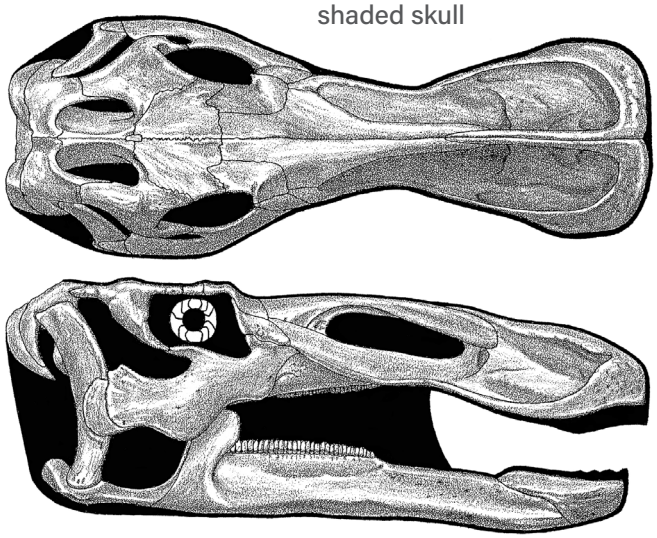
HABITS Head crests when present used for competitive visual and vocal display within species; they did not improve the sense of smell.

— HADROSAURINES OR SAUROLOPHINES

LARGE TO GIGANTIC HADROSAURIDS LIMITED TO THE LATE CRETACEOUS OF THE NORTHERN HEMISPHERE.

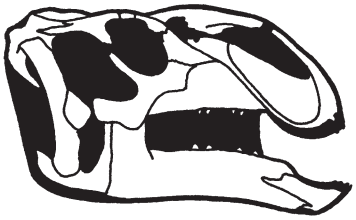
ANATOMICAL CHARACTERISTICS Very uniform except for heads. Heads fairly shallow, subrectangular, snouts long, nasal openings large.
NOTES Whether this group is hadrosaurines or saurolophines depends on uncertain placement of *Hadrosaurus* relative to other hadrosaurs. This group may be splittable into a number of subdivisions. Among dinosaurs only hadrosaurines matched some sauropods in size.

Edmontosaurus
shaded skull



Eotrachodon orientalis
— Adult size uncertain
FOSSIL REMAINS Skull and partial skeleton.

ANATOMICAL CHARACTERISTICS Head moderately deep, crest apparently absent.
AGE Late Cretaceous, late Santonian.
DISTRIBUTION AND FORMATION/S Alabama; lower Mooreville Chalk.
HABITAT/S Found as drift in nearshore marine sediments.



Eotrachodon orientalis

Hadrosaurus foulkii

— 7 m (23 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S New Jersey; middle Woodbury.
NOTES Found as drift in nearshore marine sediments.

Wulagasaurus dongi

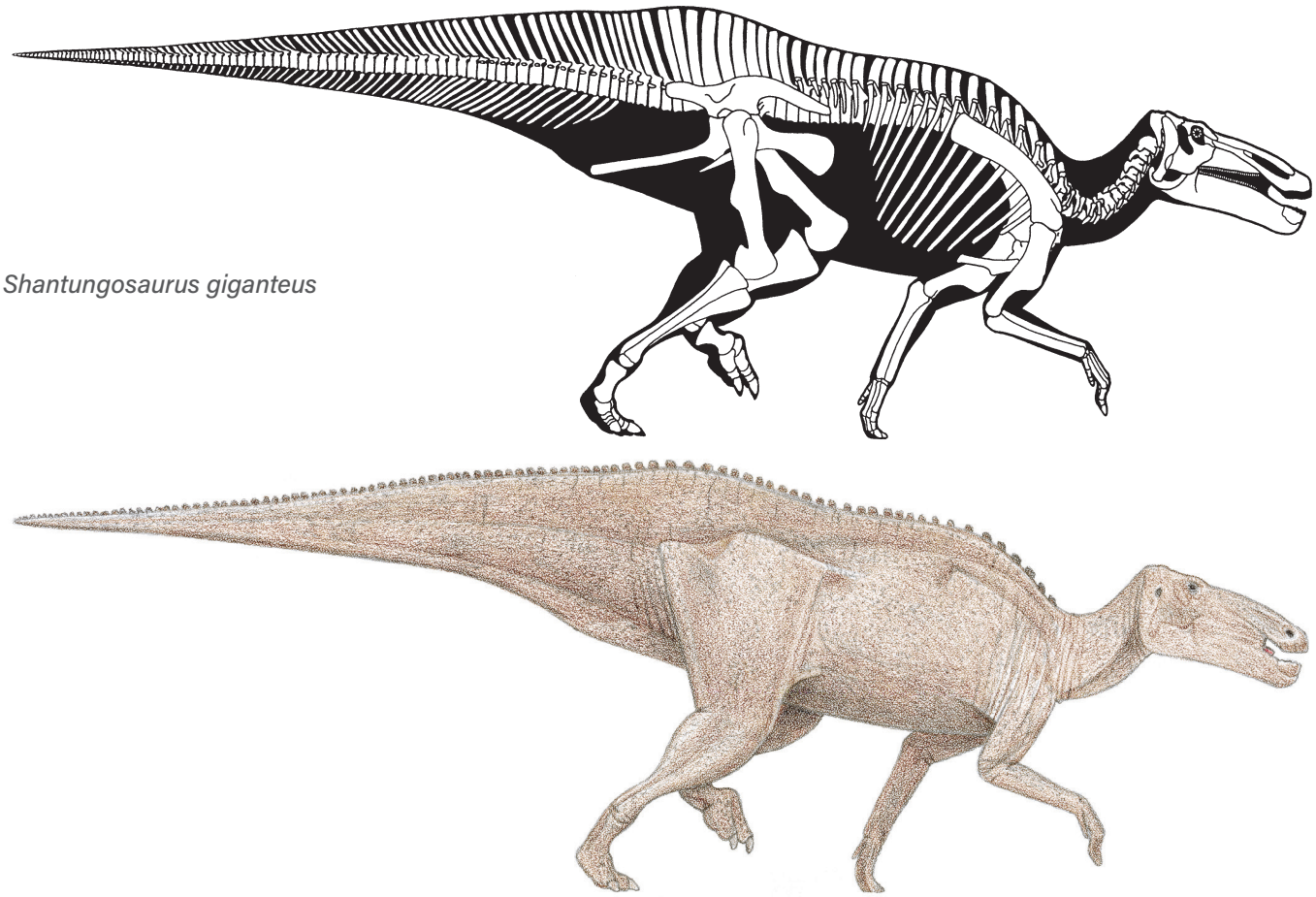
— 9 m (30 ft) TL, 3 tonnes
FOSSIL REMAINS Numerous skull and skeletal bones.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, Maastrichtian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yuliangze.

Barsboldia sicinskii

— 10 m (34 ft) TL, 5 tonnes
FOSSIL REMAINS Minority of skeleton.
ANATOMICAL CHARACTERISTICS Tall vertebral spines over trunk and tail form a low sail.
AGE Late Cretaceous, late Campanian and/or earliest Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.

Shantungosaurus giganteus

— 15 m (50 ft) TL, 13.5 tonnes
FOSSIL REMAINS Several partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Snout long, beak moderately broad, squared off, bony crest absent, lower jaw fairly deep.



Shantungosaurus giganteus

AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; upper Xingezhuang, lower and middle Hongtuya?
HABITS Middle- and low-level browser and grazer.
NOTES May include *Zhuchengosaurus maximus*, *Huaxiaosaurus aigahtens*. Some size estimates are somewhat exaggerated, but is among the largest known ornithischians, being approached by *Edmontosaurus copei*, and rivals some sauropods. Presence of soft-tissue head crest uncertain.

Kamuysaurus japonicus

— 8 m (26 ft) TL, 2.5 tonnes
FOSSIL REMAINS Partial skull and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, early Maastrichtian.
DISTRIBUTION AND FORMATION/S Southern Japan; middle Hakobuchi.

Kundurosaurus nagornyi

— 7 m (23 ft) TL, 2 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, probably late Maastrichtian.
DISTRIBUTION AND FORMATION/S Eastern Siberia: Udurchukan.

Edmontosaurus (= *Ugrunaaluk*) *kuukpikensis*

— Adult size uncertain
FOSSIL REMAINS Bone bed, almost all immature.
ANATOMICAL CHARACTERISTICS Insufficient information.

Edmontosaurus (= *Ugrunaaluk*) *kuukpikensis*

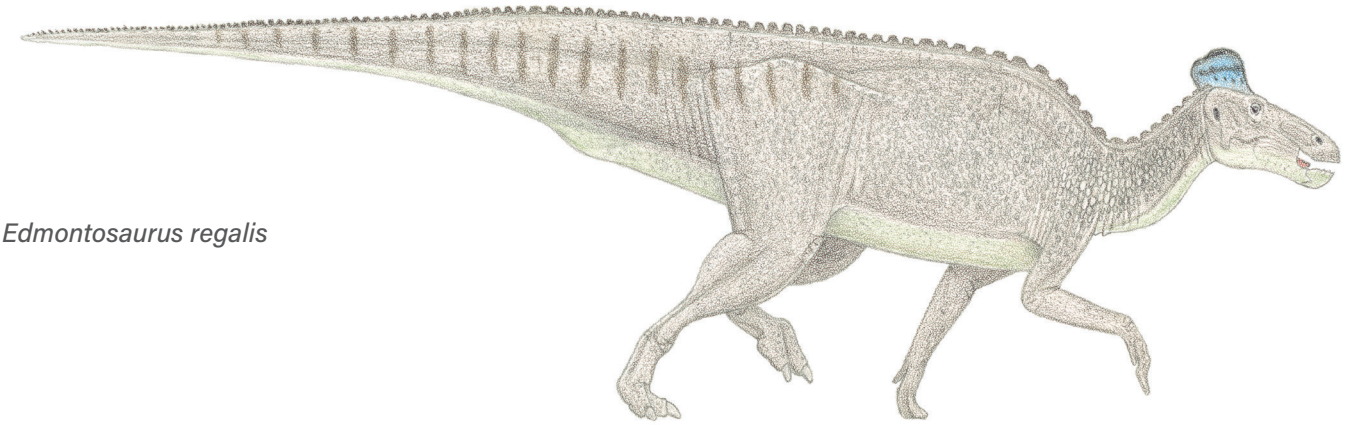
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Northern Alaska; middle Prince Creek.
HABITAT/S Well-watered coastal woodland, cool summers, severe winters including heavy snows.

Edmontosaurus regalis

— 9 m (30 ft) TL, 3.8 tonnes
FOSSIL REMAINS Numerous complete and partial skulls and skeletons.
ANATOMICAL CHARACTERISTICS Head sometimes deep, snout short because gap between beak and tooth rows is such, beak broad, rounded, shovel shaped, bony crest absent. Medium-sized, rounded, subtriangular soft-tissue crest atop back of head, pavement of large, vertically oblong scales adorns base of neck.
AGE Late Cretaceous, latest Campanian and early Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; lower Horseshoe Canyon, Saint Mary River.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
HABITS Middle- and low-level browser and occasional grazer.
NOTES That the relatively deepest heads with shortest beaks are not the very largest individuals may indicate presence of more than one species, especially if there is a stratigraphic correlation, or be a gender-related dimorphism. Head crest may have been on one gender (if so, probably male).

Edmontosaurus copei?

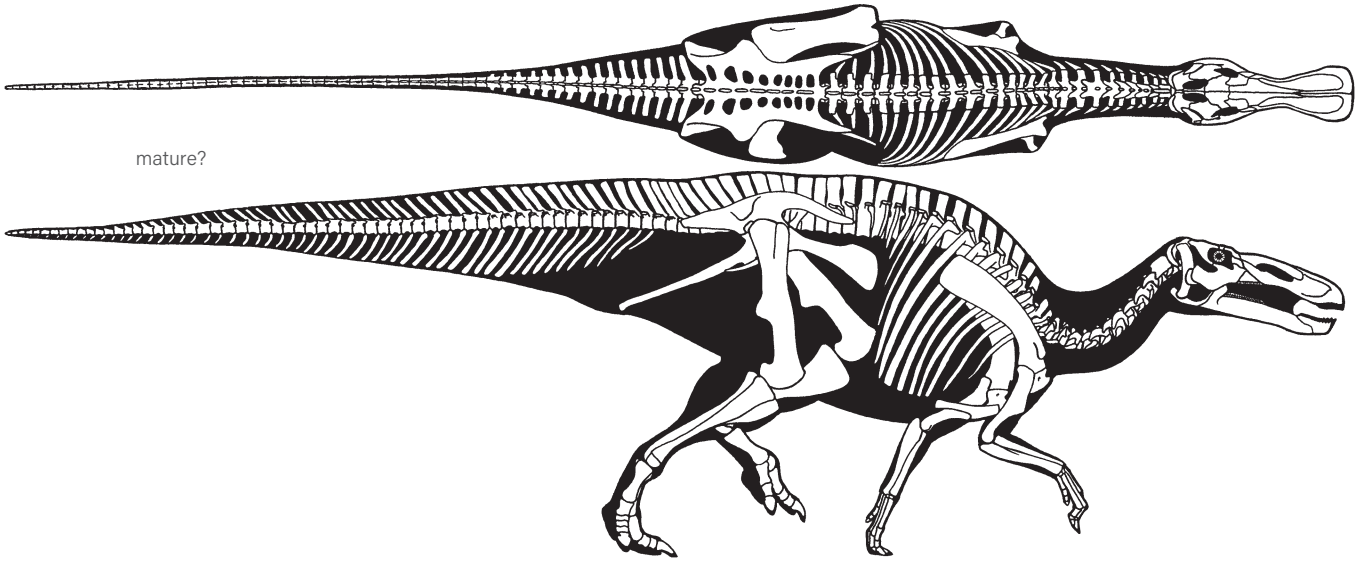
— 14 m (45 ft) TL, 13 tonnes
FOSSIL REMAINS Three complete skulls and skeletons of varying completeness, bone beds, completely known.
ANATOMICAL CHARACTERISTICS Head shallow and very elongated, snout very long because gap between beak and



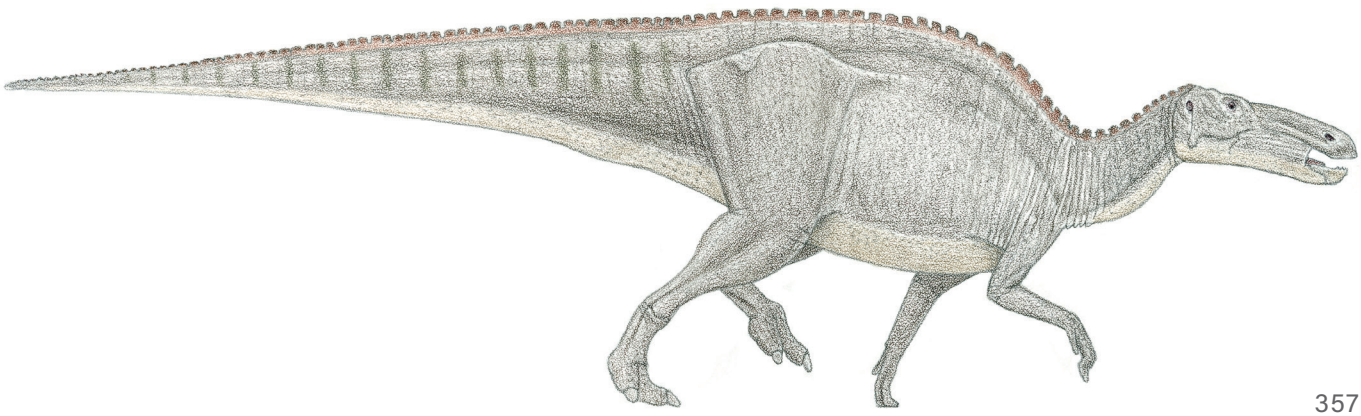
Edmontosaurus regalis

tooth rows is such, beak broad, squared, shovel shaped, tooth rows short, bony crest absent.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S South Dakota, Montana; lower? Lance and Hell Creek.
HABITAT/S Well-watered coastal woodlands.
HABITS Square muzzle at end of very long snout is an adaptation for reaching down to and mowing ground cover, the most extreme such adaptation in dinosaurs, approached only by some square-mouthed sauropods. Tooth microwear supports consuming grit-covered low plants. Also able to browse at low and medium levels.
NOTES The classic "duck-billed" hadrosaur, not different enough from *E. annectens*, etc., to be genus *Anatotitan*. Presence of all stratigraphically placed fossils from lower formation levels and absence from higher Canadian sediments suggest this was a distinct species restricted to lower levels of formations, in which case these could not be the adults of *E. annectens* for that and other reasons. If not present in latest Maastrichtian, indicates that the broad grazing beak was not successful in the long term. Bone beds containing up to dozens or hundreds of individuals suggest was a common component of fauna. Matched *Shantungosaurus* as largest ornithischian. Presence of soft-tissue head crest uncertain.

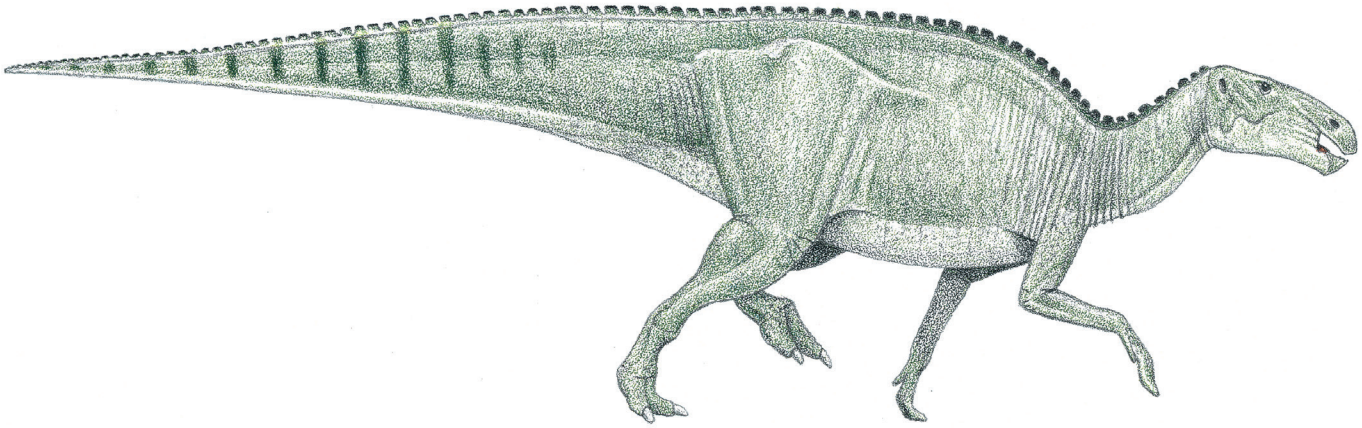
Edmontosaurus annectens
— Adult size uncertain
FOSSIL REMAINS Numerous complete and partial skulls and skeletons including several "mummies," a few juveniles, completely known.
ANATOMICAL CHARACTERISTICS Head low, elongated, snout very moderately long because gap between beak and tooth rows is such, beak broad, squared, shovel shaped, bony crest absent. Rectangular serrations along back, each corresponding to a vertebral spine at least along tail, full extent uncertain.
AGE Late Cretaceous, latest Maastrichtian.
DISTRIBUTION AND FORMATION/S Colorado, Wyoming, South Dakota, Montana, Alberta, Saskatchewan; upper Lance, upper Hell Creek, Laramie, Scollard, Frenchman, etc.
HABITAT/S Well-watered coastal woodlands.



Edmontosaurus copei?



Edmontosaurus annectens



HABITS Not as extremely adapted for grazing as earlier *E. copei*.
NOTES *E. saskatchewanensis* appears to be a juvenile of this taxon; *Anatosaurus* is a junior synonym. May not have been as common as *E. copei*. Apparent lack of giant fossils may be due to insufficient sampling. Appears to be last known hadrosaur of western North America. Healed bite marks on tops of tails verify that main enemy was *Tyrannosaurus*.

Bonapartesaurus rionegrensis

— 7 m (22 ft) TL, 1.7 tonnes
FOSSIL REMAINS Partial skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Central Argentina; lower Allen.
HABITAT/S Semiarid coastline.

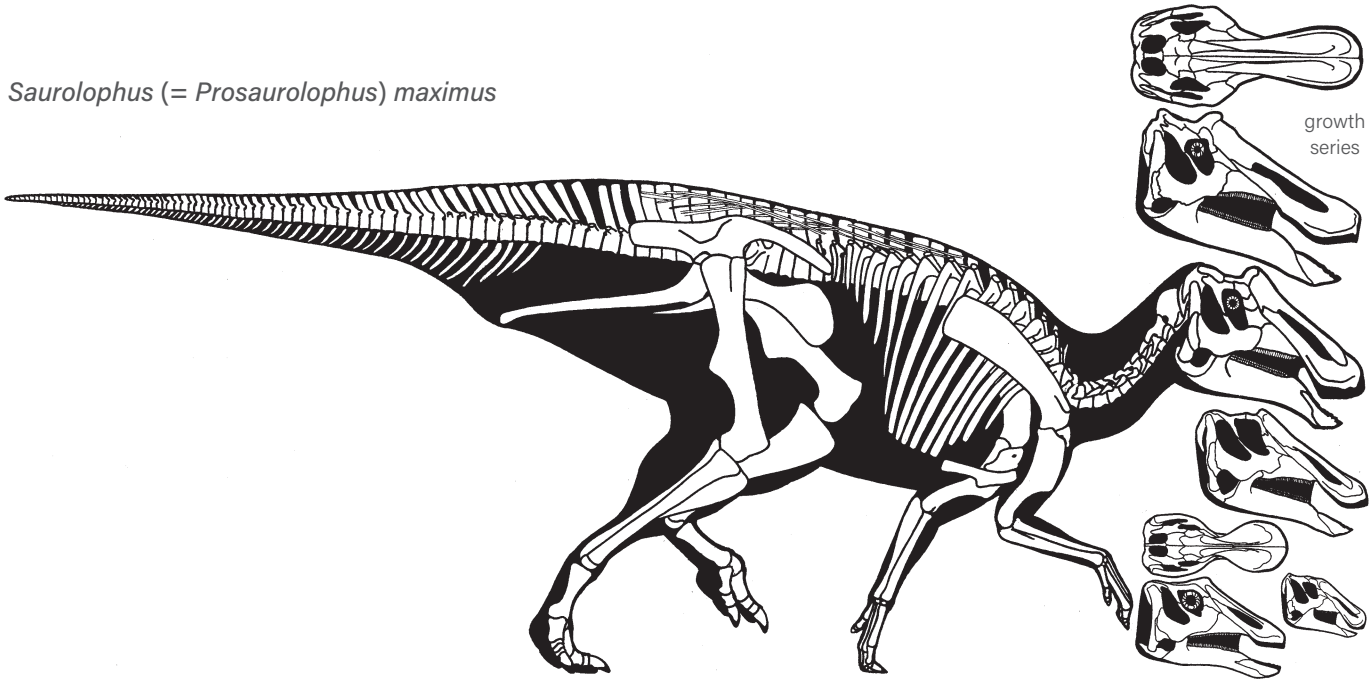
Saurolophus (= *Prosaurolophus*) *maximus*

— 8.5 m (27 ft) TL, 5 tonnes
FOSSIL REMAINS A number of skulls and skeletons of varying completeness, adult to juvenile, completely known.
ANATOMICAL CHARACTERISTICS Beak spoon shaped, shallow transverse crest over orbits.
AGE Late Cretaceous, middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Dinosaur Park, upper Two Medicine, lower Bearpaw.
HABITAT/S Well-watered, forested floodplains with coastal swamps and marshes, cool winters.
NOTES *S. blackfeetensis* is probably a juvenile of this species, fossils from higher strata may be a distinct species.

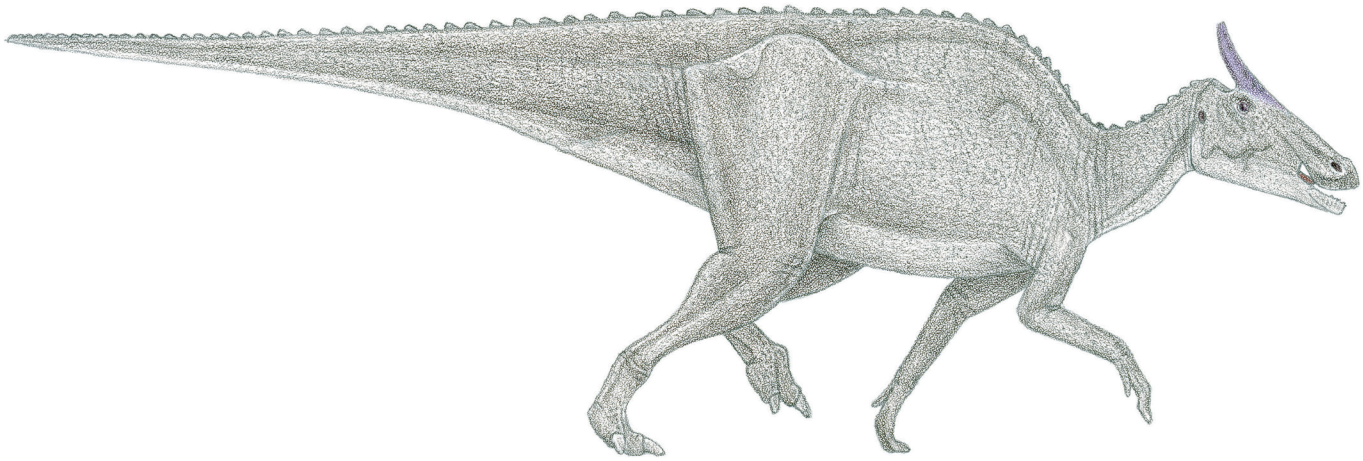
Saurolophus osborni

— 8.5 m (27 ft) TL, 3 tonnes
FOSSIL REMAINS Two complete skulls and a nearly complete skeleton, almost completely known.
ANATOMICAL CHARACTERISTICS Beak spoon shaped, spike-shaped crest over orbits.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be the direct descendant of *S. maximus*.

Saurolophus (= *Prosaurolophus*) *maximus*



Saurolophus osborni

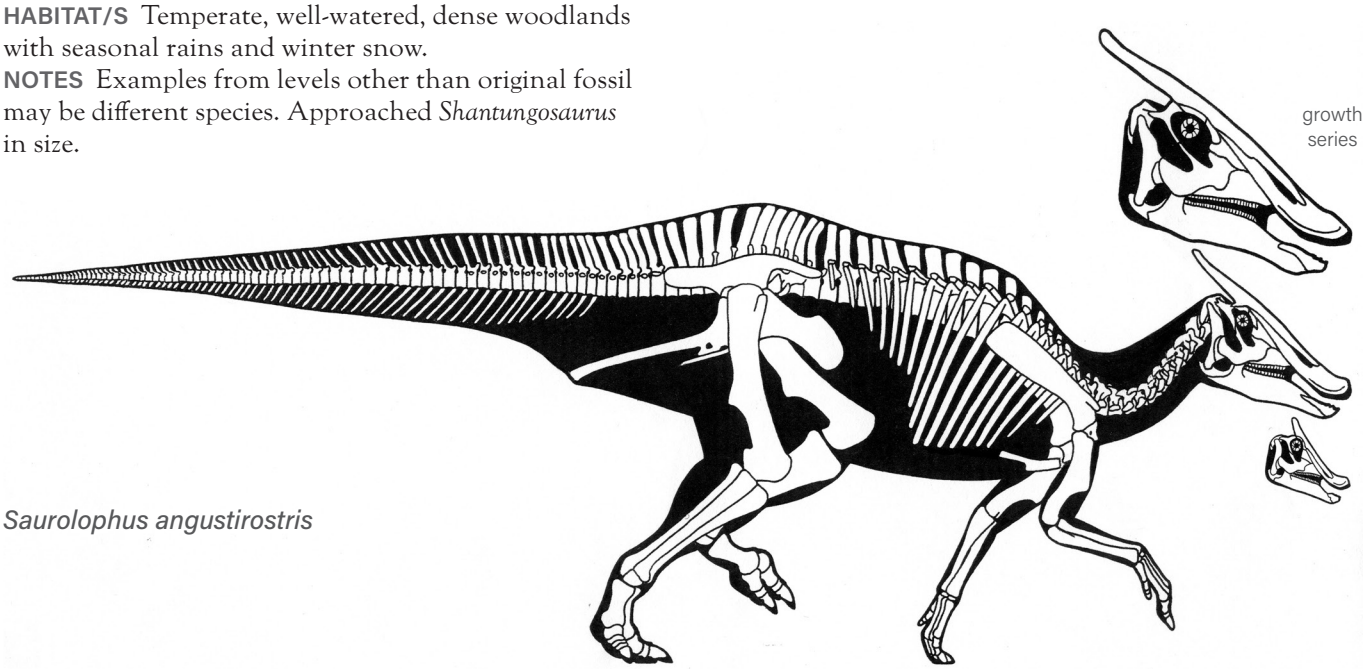


Saurolophus (= *Augustynolophus*) *morrisi*
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Beak spoon shaped, spike-shaped crest over orbits.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S California; Moreno.

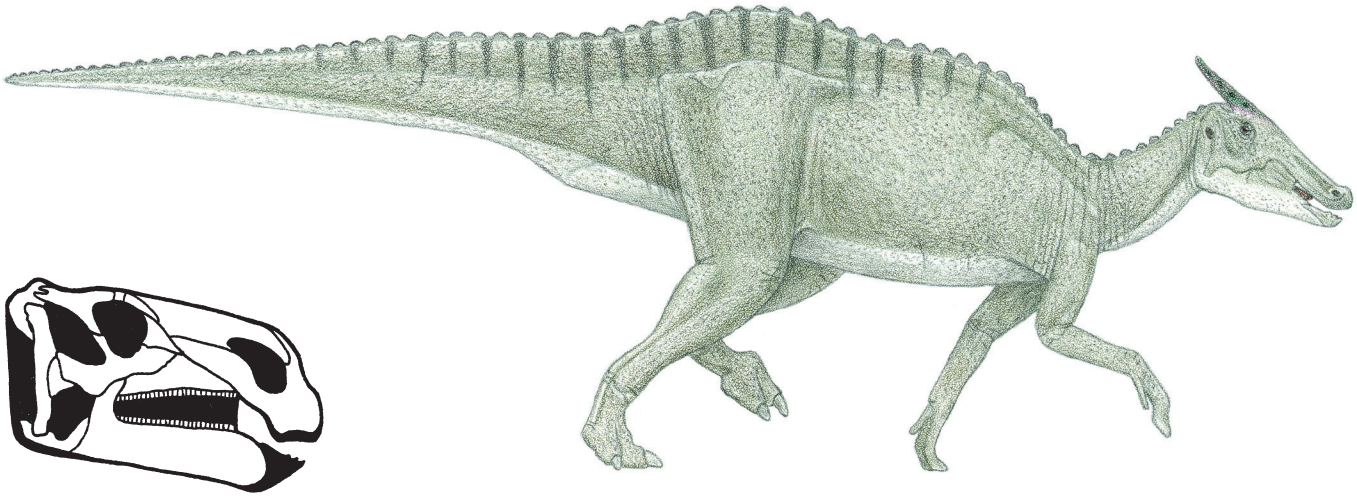
Saurolophus angustirostris
— 13 m (43 ft) TL, 11 tonnes
FOSSIL REMAINS Complete skull and numerous skeletons, almost completely known.
ANATOMICAL CHARACTERISTICS Beak spoon shaped, spike-shaped crest over orbits.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Mongolia; lower? Nemegt.
HABITAT/S Temperate, well-watered, dense woodlands with seasonal rains and winter snow.
NOTES Examples from levels other than original fossil may be different species. Approached *Shantungosaurus* in size.

Acristavus gagslarsoni
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS Majority of skull.
ANATOMICAL CHARACTERISTICS Front edge of upper beak indented, bony crest absent.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; lower Two Medicine.

Maiasaura (or *Brachylophosaurus*) *peeblesorum*
— 7 m (23 ft) TL, 2.5 tonnes
FOSSIL REMAINS Several complete skulls and majority of skeletons, bone beds, juvenile to adult, numerous nests, completely known.
ANATOMICAL CHARACTERISTICS Beak narrow, squared off, shallow transverse crest over orbits. Spherical eggs 10 cm (4 in) in diameter.

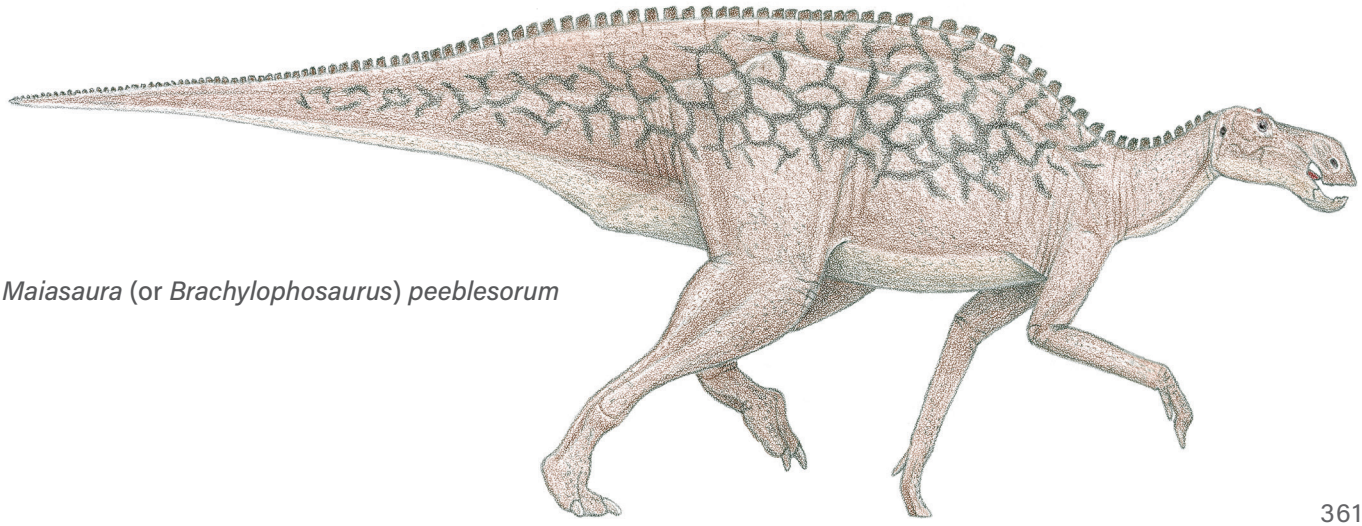


Saurolophus angustirostris



Acristavus gagslarsoni

Maiasaura (or *Brachylophosaurus*) *peeblesorum*



Maiasaura (or *Brachylophosaurus*) *peeblesorum*

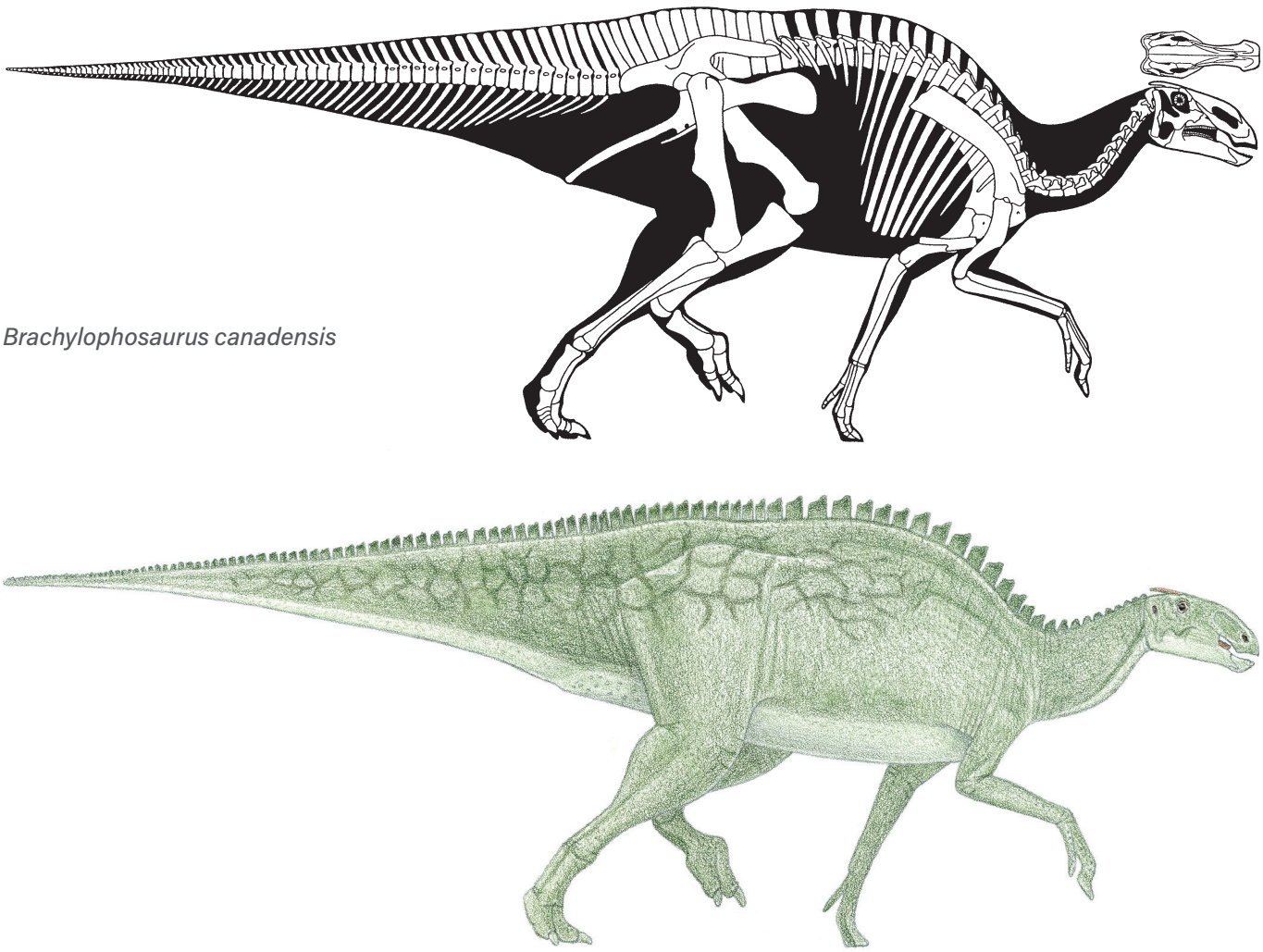
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Montana, Alberta?; middle Two Medicine, upper Oldman?
HABITAT/S Seasonally dry upland woodlands.
HABITS Middle- and low-level browser. Bone beds indicate at least sometimes congregated in large herds. May have nested in colonies, hatchlings apparently remained in nest during first weeks of growth, probably fed by parents. Transverse head crest best suited for frontal displays with head not strongly pitched down.
NOTES Alberta remains may be same species. May be a subgenus of *Brachylophosaurus*.

Brachylophosaurus (= *Probrachylophosaurus*) *bergei*

— 10 m (33 ft) TL, 5 tonnes
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Small horizontal platelike crest over rear of head.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Montana; middle Judith River.
HABITS Transverse head crest best suited for frontal displays with head strongly pitched down.
NOTES The new genus title for this species so similar to *B. canadensis* is a classic example of generic oversplitting. May be direct ancestor of *B. canadensis*.

Brachylophosaurus canadensis

— 11 m (35 ft) TL, 7 tonnes
FOSSIL REMAINS Several complete skulls and skeletons, including mummy, completely known.
ANATOMICAL CHARACTERISTICS Head rather small, beak narrow, squared off, flat, platelike crest over rear of head. Hatchet-shaped serrations along back, each corresponding to a vertebral spine, full extent uncertain.
AGE Late Cretaceous, late middle Campanian.
DISTRIBUTION AND FORMATION/S Alberta; upper Oldman, lower Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes.
HABITS Middle- and low-level browser. Transverse head crest best suited for frontal displays with head strongly pitched down.



Brachylophosaurus canadensis

NOTES Fossil from the Foremost Formation usually placed in this taxon is probably an earlier species.

Kritosaurus (or *Gryposaurus*) *notabilis*

— 8 m (26 ft) TL, 3.4 tonnes

FOSSIL REMAINS A number of complete and partial skulls and skeletons, adult to juvenile, completely known.

ANATOMICAL CHARACTERISTICS Long, shallow crest ridge over nasal opening well developed, beak narrow, rounded. Large conical serrations along back do not correspond to neural spines, full extent uncertain.

AGE Late Cretaceous, late middle Campanian.

DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park.

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

HABITS Middle- and low-level browser.

NOTES Probably includes immature *K. incurvimanus*. Because the skulls and skeletons of kritosaurs are very similar except for the crest, they probably form one genus; *Gryposaurus* may be a subgenus.

Kritosaurus (or *Gryposaurus*) *latidens*

— 7.5 m (25 ft) TL, 3 tonnes

FOSSIL REMAINS Partial skulls and majority of skeleton.

ANATOMICAL CHARACTERISTICS Long, shallow crest ridge over nasal opening moderately developed.

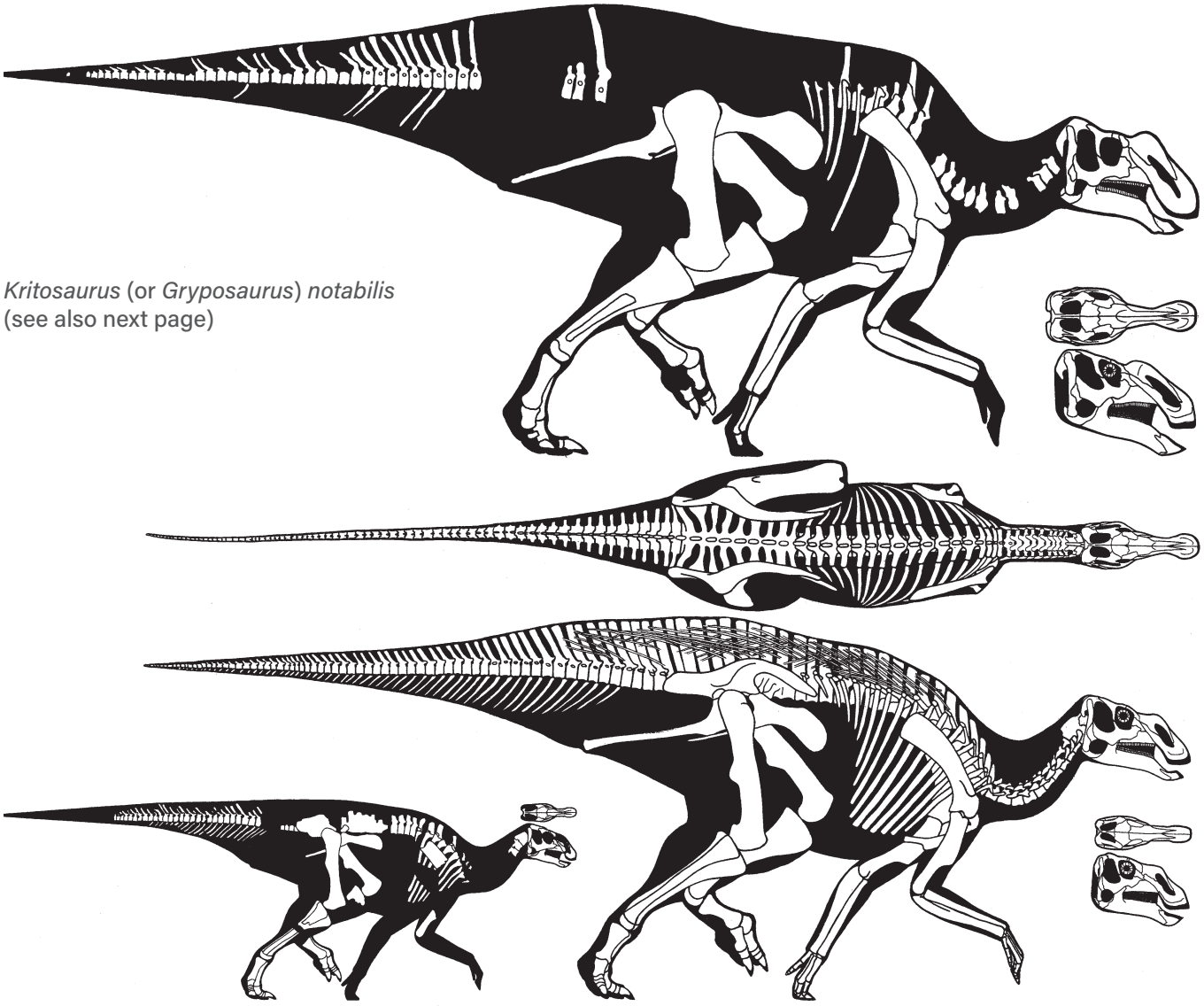
AGE Late Cretaceous, middle Campanian.

DISTRIBUTION AND FORMATION/S Montana; lower Two Medicine.

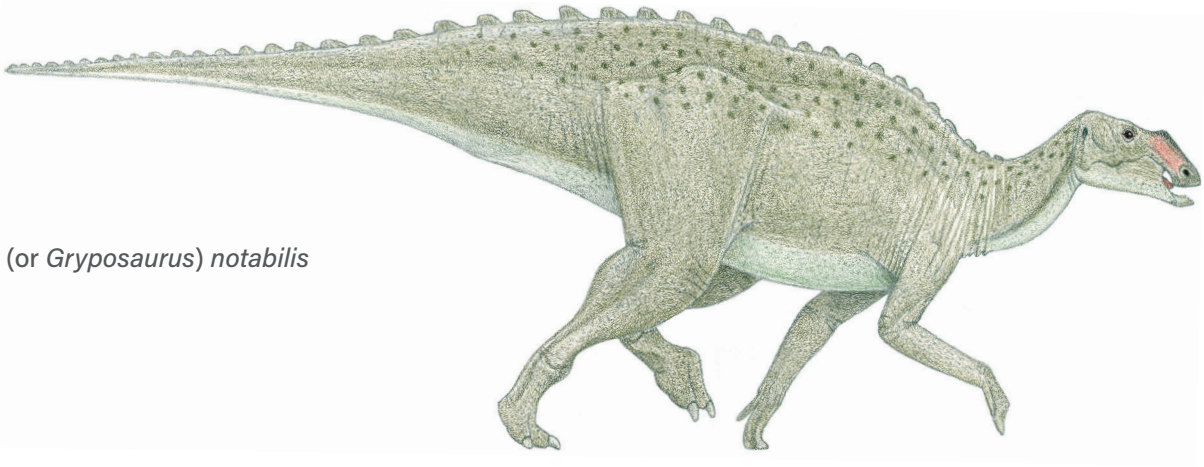
HABITAT/S Seasonally dry upland woodlands.

HABITS Middle- and low-level browser.

NOTES May be ancestral to at least some of the kritosaurs listed below from the same region.



Kritosaurus (or *Gryposaurus*) *notabilis*
(see also next page)



Kritosaurus (or *Gryposaurus*) *notabilis*

Kritosaurus (or *Gryposaurus*) *monumentensis*

— 8 m (26 ft) TL, 3 tonnes

FOSSIL REMAINS Majority of skull and skeleton.

ANATOMICAL CHARACTERISTICS Head and skeleton heavily built. Head exceptionally deep and vertical; long, shallow crest ridge over nasal opening well developed.

AGE Late Cretaceous, middle Campanian.

DISTRIBUTION AND FORMATION/S Utah; middle Kaiparowits.

HABITS Depth and strength of head and of jaw muscles indicate ability to process coarse vegetation.

NOTES May be direct ancestor of *K. condrupus*.

Kritosaurus (or *Rhinorex*) *condrupus*

— 7 m (23 ft) TL, 2.5 tonnes

FOSSIL REMAINS Majority of skull and skeleton.

ANATOMICAL CHARACTERISTICS Head deep, snout strongly downturned.

AGE Late Cretaceous, early late Campanian.

DISTRIBUTION AND FORMATION/S Utah; lower Neslen.

HABITS Depth of head and strength of jaw muscles indicate ability to process coarse vegetation.

NOTES May be direct ancestor of *K. navajovius*.

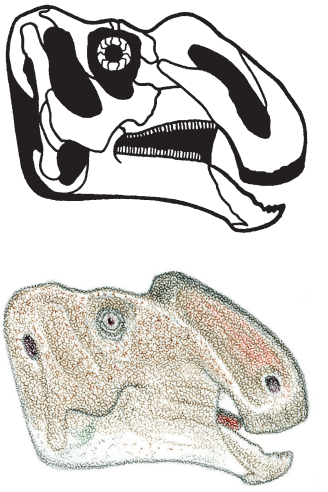
Kritosaurus navajovius

— 9 m (30 ft) TL, 4 tonnes

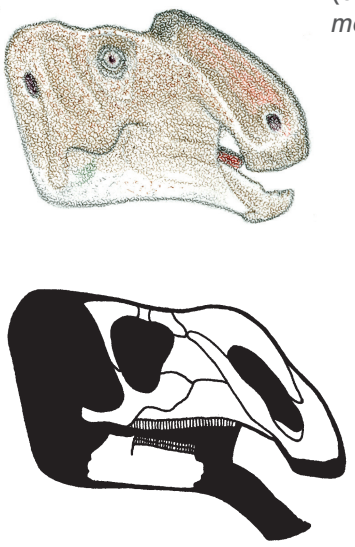
FOSSIL REMAINS Partial skull.

ANATOMICAL CHARACTERISTICS Insufficient information.

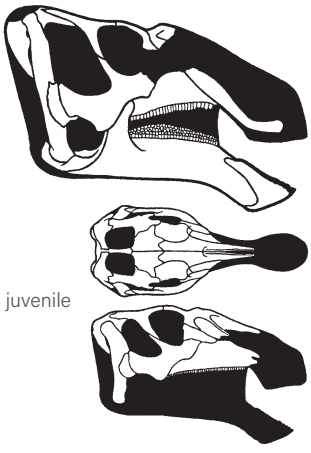
AGE Late Cretaceous, late Campanian.



Kritosaurus (or *Gryposaurus*) *monumentensis*



Kritosaurus (or *Rhinorex*) *condrupus*



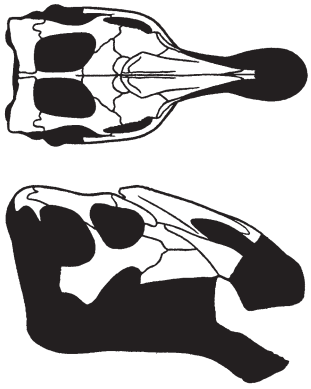
juvenile

Kritosaurus navajovius

DISTRIBUTION AND FORMATION/S New Mexico; lower Kirtland.
HABITAT/S Moderately watered floodplain woodlands, coastal swamps, and marshes.
NOTES *Naashoibitosaurus ostromi* may be an immature member of this species.

Kritosaurus (or *Anasazisaurus*) *horneri*

— 7.5 m (25 ft) TL, 2.5 tonnes
FOSSIL REMAINS Partial skull.
ANATOMICAL CHARACTERISTICS Long, shallow crest ridge over nasal opening with small hook at back end.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; lower Kirtland.
HABITAT/S Moderately watered floodplain woodlands, coastal swamps, and marshes.



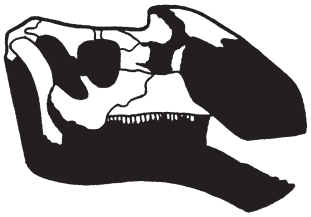
Kritosaurus (or *Anasazisaurus*) *horneri*

Aquilarhinus (or *Kritosaurus*) *palimentus*

— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton, immature.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, lower Campanian.
DISTRIBUTION AND FORMATION/S Southern Texas; lower Aguja.

Aralosaurus (or *Kritosaurus*) *tuberiferus*

— Adult size uncertain
FOSSIL REMAINS Partial skull, possibly a large juvenile.
ANATOMICAL CHARACTERISTICS Long, prominent crest ridge over nasal opening with incipient hook at back end.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Kazakhstan; Beleuta Svita.



Aralosaurus (or *Kritosaurus*) *tuberiferus*

Secernosaurus koerneri

— Adult size uncertain
FOSSIL REMAINS Minority of skeleton, probably juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Cenomanian or Turonian.
DISTRIBUTION AND FORMATION/S Southern Argentina; lower Bajo Barreal.
HABITAT/S Seasonally wet, well-forested floodplain.
NOTES This and *Willinakaqe* probably form a distinct South American hadrosaur group.

Willinakaqe salitralensis

— 7 m (23 ft) TL, 2 tonnes
FOSSIL REMAINS Partial skull and skeletons.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Campanian and/or early Maastrichtian.
DISTRIBUTION AND FORMATION/S Central Argentina; lower Allen.
HABITAT/S Semiarid coastline.

— LAMBEOSAURINES

LARGE TO GIGANTIC HADROSAURIDS LIMITED TO LATE CRETACEOUS OF THE NORTHERN HEMISPHERE.

ANATOMICAL CHARACTERISTICS Very uniform except for head crests, which are always atop back of head and contain looping segments of nasal passages. Heads subtriangular, snouts slender, beaks narrow and rounded, nasal openings narrow.
HABITS Middle- and low-level browsers. Crests may have been used to help generate vocal sounds for display and communication.

Nanningosaurus dashiensis
— 7.5 m (25 ft) TL, 3 tonnes
FOSSIL REMAINS Minority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Late Cretaceous.
DISTRIBUTION AND FORMATION/S Southern China; unnamed.

Pararhabdodon isonensis
— Adult size uncertain
FOSSIL REMAINS Minority of skull and skeletons.
ANATOMICAL CHARACTERISTICS Lower jaw strongly downcurved and unusually broad, indicating head was wider than usual in hadrosaurs.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Northeastern Spain; Tremp.
NOTES Probably includes *Koutalisaurus kohlerorum*.

Arenysaurus ardevoli
— 6 m (20 ft) TL, 1.5 tonnes
FOSSIL REMAINS Partial skull and skeleton.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Northeastern Spain; Tremp.

Angulomastacator daviesi
— Size uncertain
FOSSIL REMAINS Minority of skull.
ANATOMICAL CHARACTERISTICS Snout strongly downturned.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Texas; upper Aguja.

Parasaurolophus cyrtocristatus
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS A few partial skulls and skeletal remains, adult and immature.
ANATOMICAL CHARACTERISTICS Short, backward-projecting, downward-arced tube crest.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; upper Fruitland.

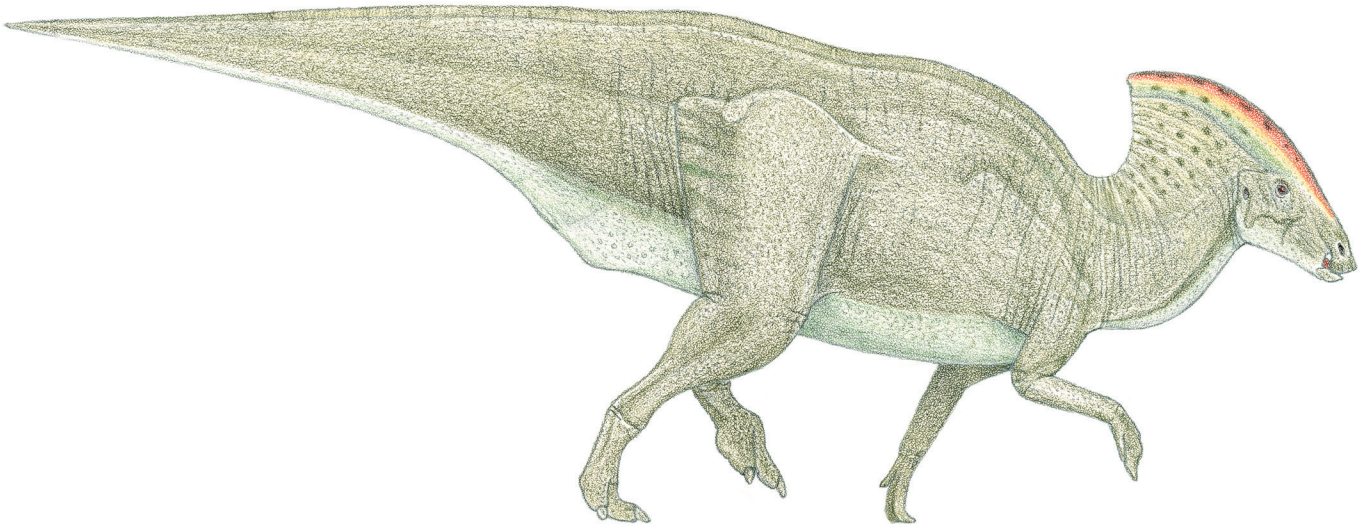
Parasaurolophus walkeri
— 7.5 m (25 ft) TL, 2.7 tonnes
FOSSIL REMAINS Complete skull and majority of skeleton, other possible remains.
ANATOMICAL CHARACTERISTICS Long, backward-projecting, downward-arced tube crest.
AGE Late Cretaceous, late middle to early late? Campanian.
DISTRIBUTION AND FORMATION/S Alberta; lower to middle? Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be an ancestor of *P. tubicen*.

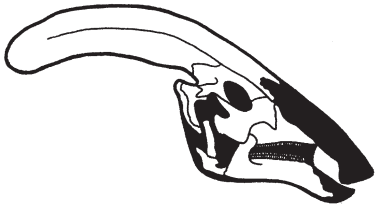
Parasaurolophus tubicen
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS A few partial skulls and skeletal remains.
ANATOMICAL CHARACTERISTICS Long, backward-projecting, downward-arced tube crest.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S New Mexico; upper Kirtland.

Charonosaurus (or *Parasaurolophus*) *jiayinensis*
— 10 m (23 ft) TL, 6 tonnes
FOSSIL REMAINS Partial skull and majority of skeletons, juveniles to adults.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Northeastern China; Yuliangze.
NOTES May have had a tubular crest like that of *Parasaurolophus*.

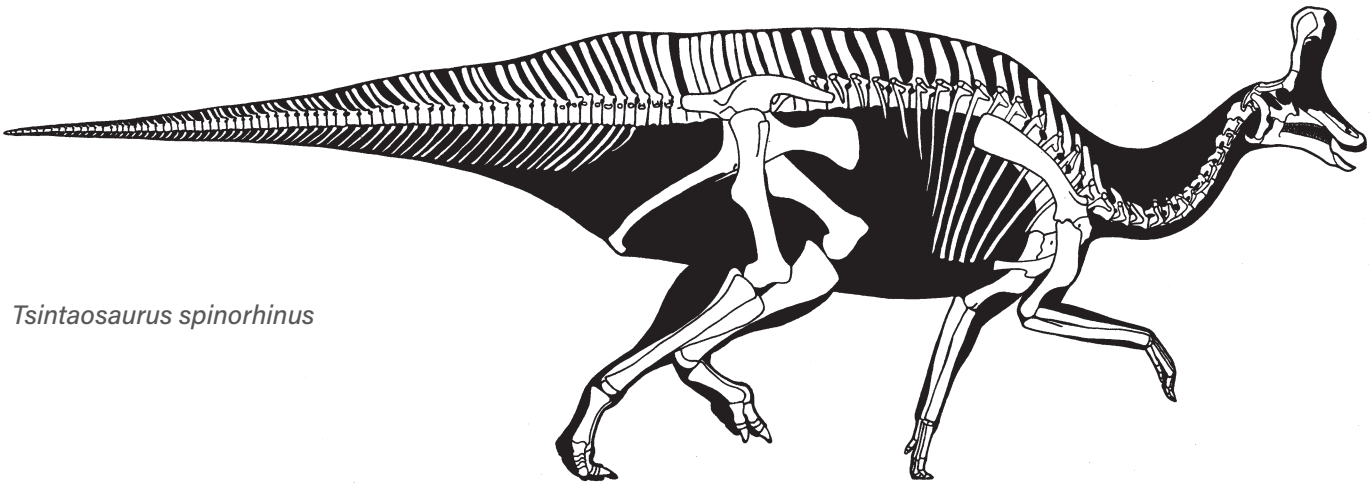
Tsintaosaurus spinorhinus
— 8.3 m (27 ft) TL, 2.7 tonnes
FOSSIL REMAINS Two partial skulls and majority of a few skeletons.

Parasaurolophus walkeri





Parasaurolophus tubicen



Tsintaosaurus spinorhinus

ANATOMICAL CHARACTERISTICS Head crest tall, subvertical, and at least fairly broad. Neck longer than usual for hadrosaurs. Arm long.
AGE Late Cretaceous, Campanian.
DISTRIBUTION AND FORMATION/S Eastern China; Jingangkou.
NOTES Crest used to be thought to be a narrow tube, full dimensions not known.

Olorotitan arharensis

— 8 m (26 ft) TL, 3.2 tonnes
FOSSIL REMAINS Majority of skull and skeleton.
ANATOMICAL CHARACTERISTICS Large, subvertical, fan-shaped crest. Neck longer than in other hadrosaurs.
AGE Late Cretaceous, late Maastrichtian.
DISTRIBUTION AND FORMATION/S Eastern Siberia; Tsagayan.
HABITS Longer neck indicates ability to browse at a relatively high level.

Nipponosaurus (or *Hypacrosaurus*) *sachaliensis*

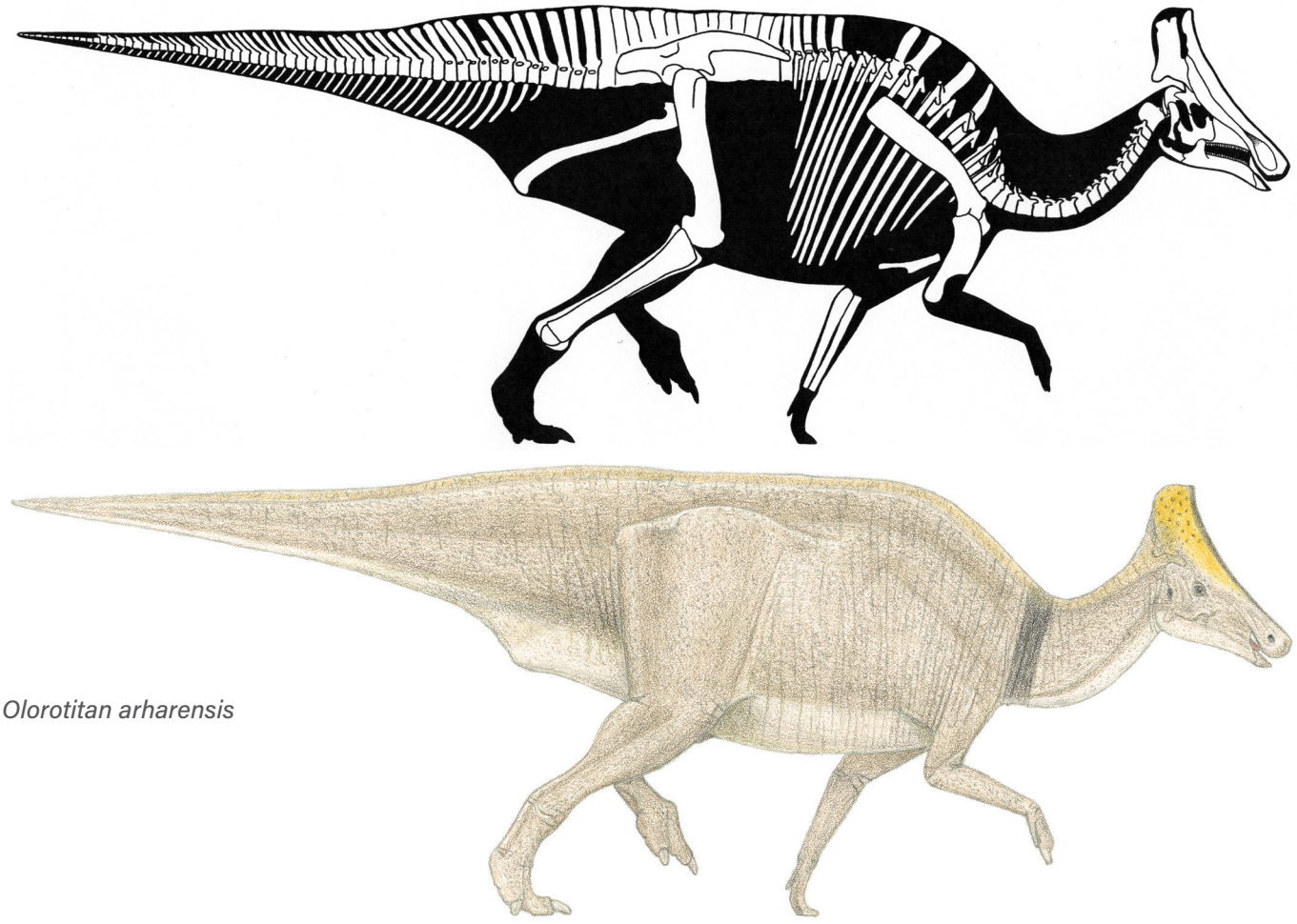
— Adult size uncertain
FOSSIL REMAINS Partial skull and skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Insufficient information.
AGE Late Cretaceous, late Santonian or early Campanian.
DISTRIBUTION AND FORMATION/S Sakhalin Island (east of Siberia); Ryugase Group.

Amurosaurus (or *Hypacrosaurus*) *riabinini*

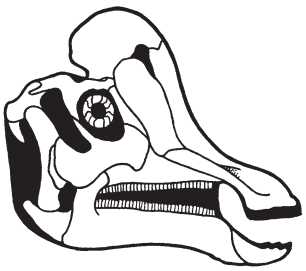
— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS Majority of skull and skeleton, numerous partial remains.
ANATOMICAL CHARACTERISTICS Large, semicircular crest atop back of skull, front end of lower jaw sharply downturned.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Eastern Siberia, northeastern China; Udurchukan, Yuliangze.
NOTES Includes *Sahaliyania elunchumorum*.

Hypacrosaurus (= *Velafrons*) *coahuilensis*

— Adult size uncertain
FOSSIL REMAINS Nearly complete skull, partial skeleton, juvenile.
ANATOMICAL CHARACTERISTICS Large, semicircular crest atop back of skull.
AGE Late Cretaceous, middle Campanian.
DISTRIBUTION AND FORMATION/S Northeastern Mexico; Cerro del Pueblo.



Olorotitan arharensis



Hypacrosaurus (= *Velafrons*) *coahuilensis*

Hypacrosaurus (= *Corythosaurus*) *casuarius*

— 8 m (26 ft) TL, 3 tonnes

FOSSIL REMAINS A number of complete skulls and skeletons, including mummies, completely known. Low ribbon frill along back appears to connect to back of head crest.

ANATOMICAL CHARACTERISTICS Large, semicircular crest atop back of skull.

AGE Late Cretaceous, late middle Campanian.

DISTRIBUTION AND FORMATION/S Alberta; lower Dinosaur Park.

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

NOTES Because the skulls and skeletons of *Hypacrosaurus*, *Corythosaurus*, and *Lambeosaurus* are very similar except for the head crest and height of the neural spines, they probably form one genus.

Hypacrosaurus (= *Corythosaurus*) *intermedius*

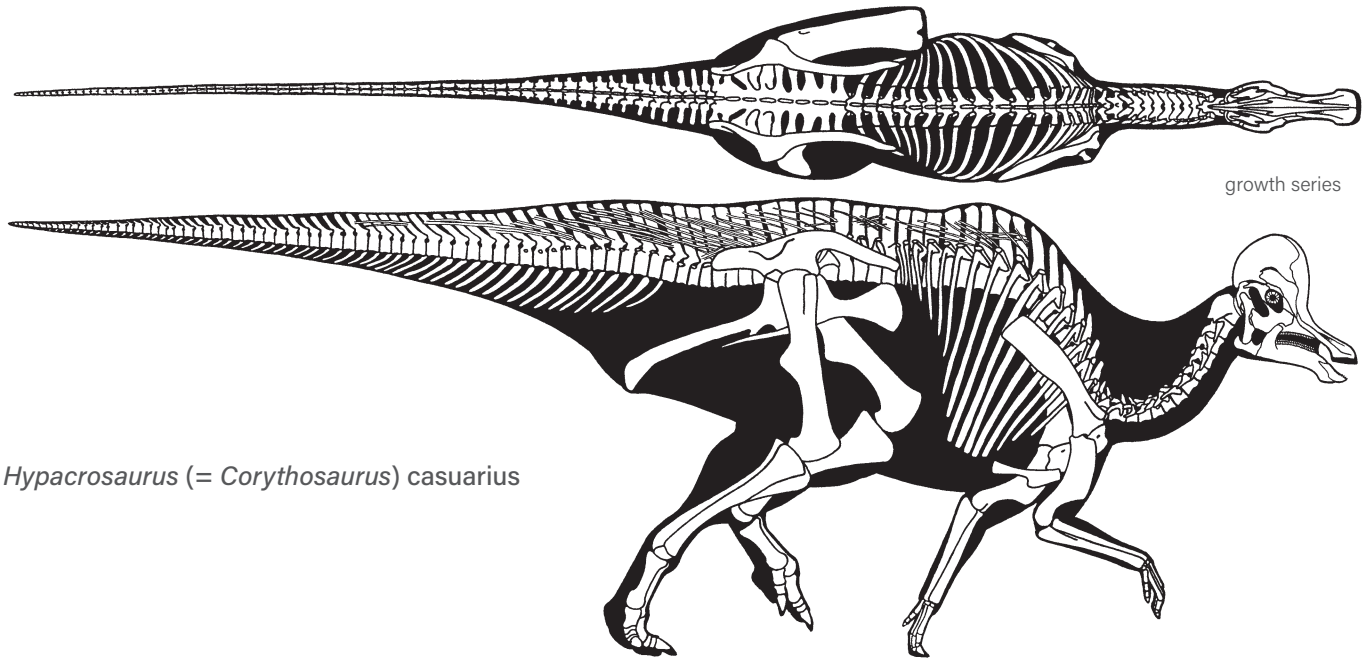
— 7.7 m (25 ft) TL, 2.7 tonnes

FOSSIL REMAINS Complete and partial skulls and skeletons.

ANATOMICAL CHARACTERISTICS Large, subtriangular crest atop back of skull.

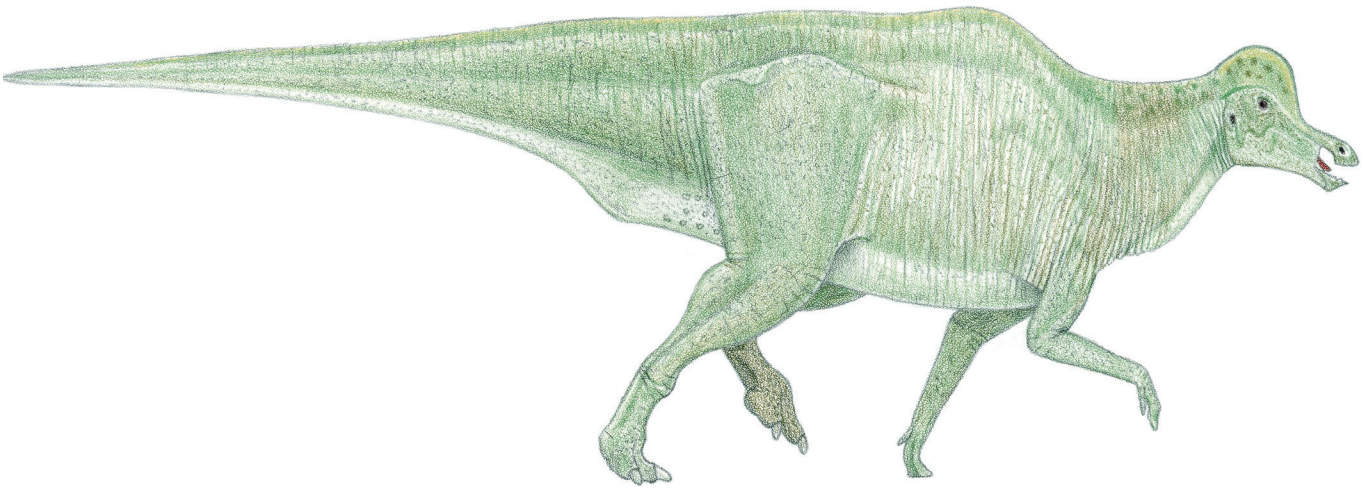
AGE Late Cretaceous, early late and middle late Campanian.

DISTRIBUTION AND FORMATION/S Alberta; middle and upper Dinosaur Park.

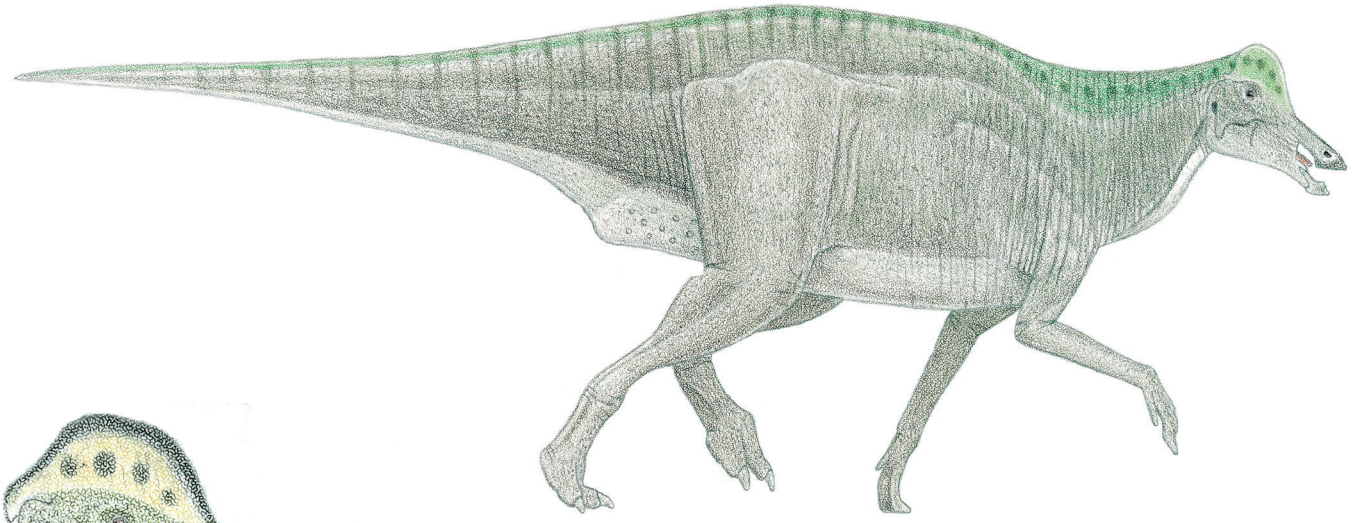


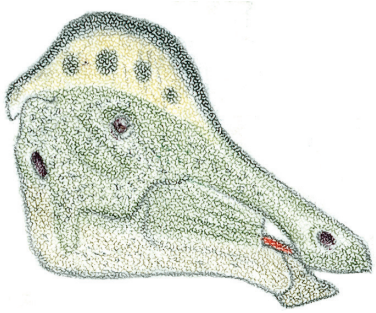
growth series

Hypacrosaurus (= *Corythosaurus*) casuarius



Hypacrosaurus (= *Corythosaurus*) *intermedius* immature





Hypacrosaurus stebingeri

HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Previously thought to be the female of earlier *H. casuarius*, may be its descendant.

Hypacrosaurus stebingeri

— 8 m (26 ft) TL, 3 tonnes
FOSSIL REMAINS Complete skull and majority of skeletons, juvenile remains including embryos, nests.
ANATOMICAL CHARACTERISTICS Large, semicircular crest atop back of skull. Tall vertebral spines over trunk form a low sail. Eggs spherical, 20 cm (8 in) in diameter.
AGE Late Cretaceous, middle and/or late Campanian.
DISTRIBUTION AND FORMATION/S Montana, Alberta; upper Two Medicine.
HABITAT/S Seasonally dry upland woodlands.

Hypacrosaurus altispinus

— 8 m (26 ft) TL, 3.6 tonnes
FOSSIL REMAINS Several skulls and partial skeletons.
ANATOMICAL CHARACTERISTICS Large, subtriangular crest atop back of skull. Tall vertebral spines over trunk form a prominent sail.
AGE Late Cretaceous, middle Maastrichtian.
DISTRIBUTION AND FORMATION/S Alberta; middle Horseshoe Canyon.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

Hypacrosaurus (*Magnapaulia*) *laticaudus*

— 9 m (30 ft) TL, 4 tonnes
FOSSIL REMAINS Partial skull and skeletons, juvenile to adult.
ANATOMICAL CHARACTERISTICS Tall vertebral spines of trunk and tail form a prominent sail.
AGE Late Cretaceous, late Campanian.
DISTRIBUTION AND FORMATION/S Baja California, Mexico; middle El Gallo.

Hypacrosaurus stebingeri

Hypacrosaurus altispinus

Hypacrosaurus (*Lambeosaurus*) *clavinitialis*

— 7.7 m (25 ft) TL, 3.4 tonnes

FOSSIL REMAINS A few complete skulls, majority of skeleton.

ANATOMICAL CHARACTERISTICS Large, hatchet-shaped crest atop back of head.

AGE Late Cretaceous, early late Campanian.

DISTRIBUTION AND FORMATION/S Alberta; middle Dinosaur Park.

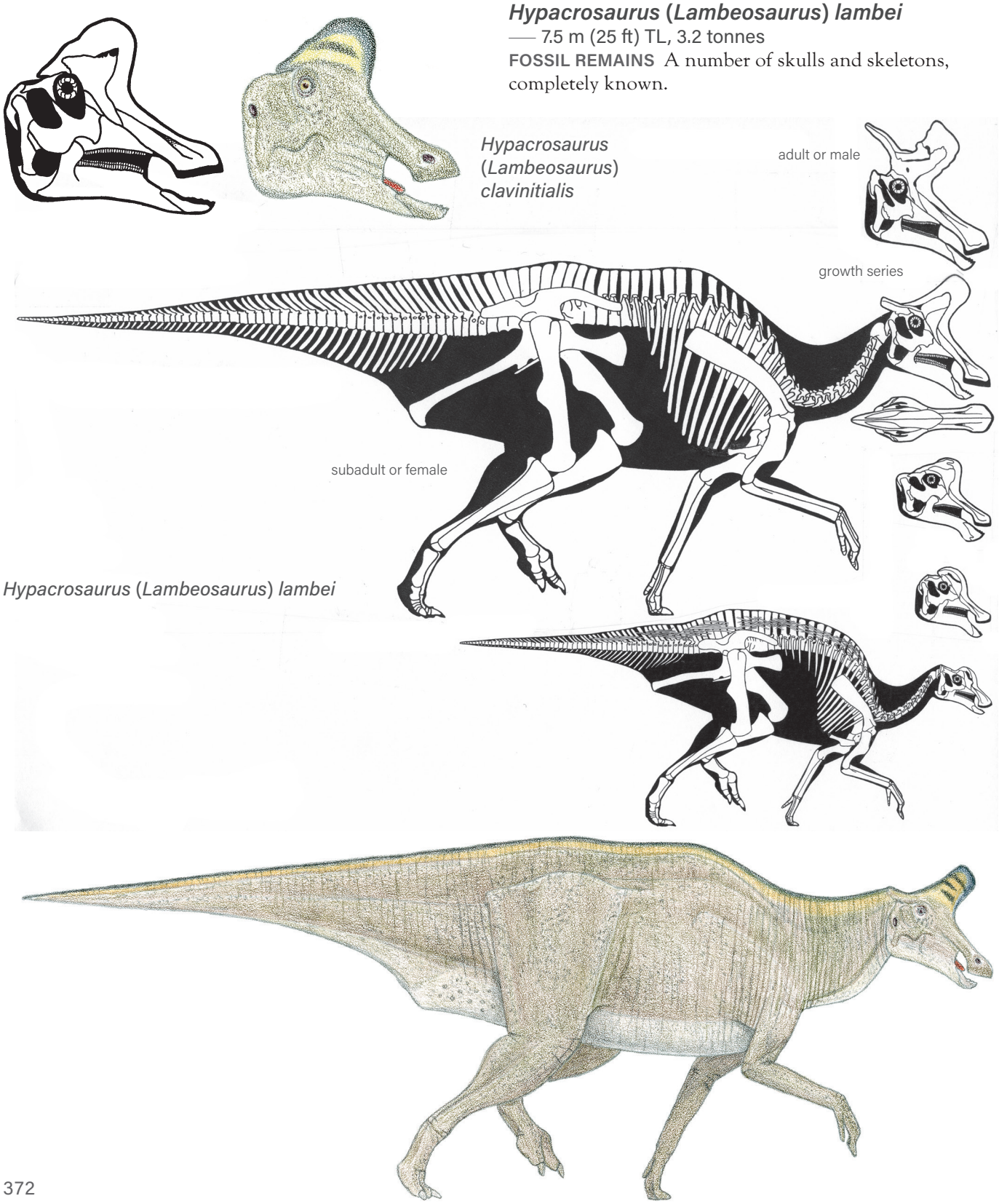
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.

NOTES Previously thought to be the female of *H. lambei*, may be its ancestor.

Hypacrosaurus (*Lambeosaurus*) *lambei*

— 7.5 m (25 ft) TL, 3.2 tonnes

FOSSIL REMAINS A number of skulls and skeletons, completely known.

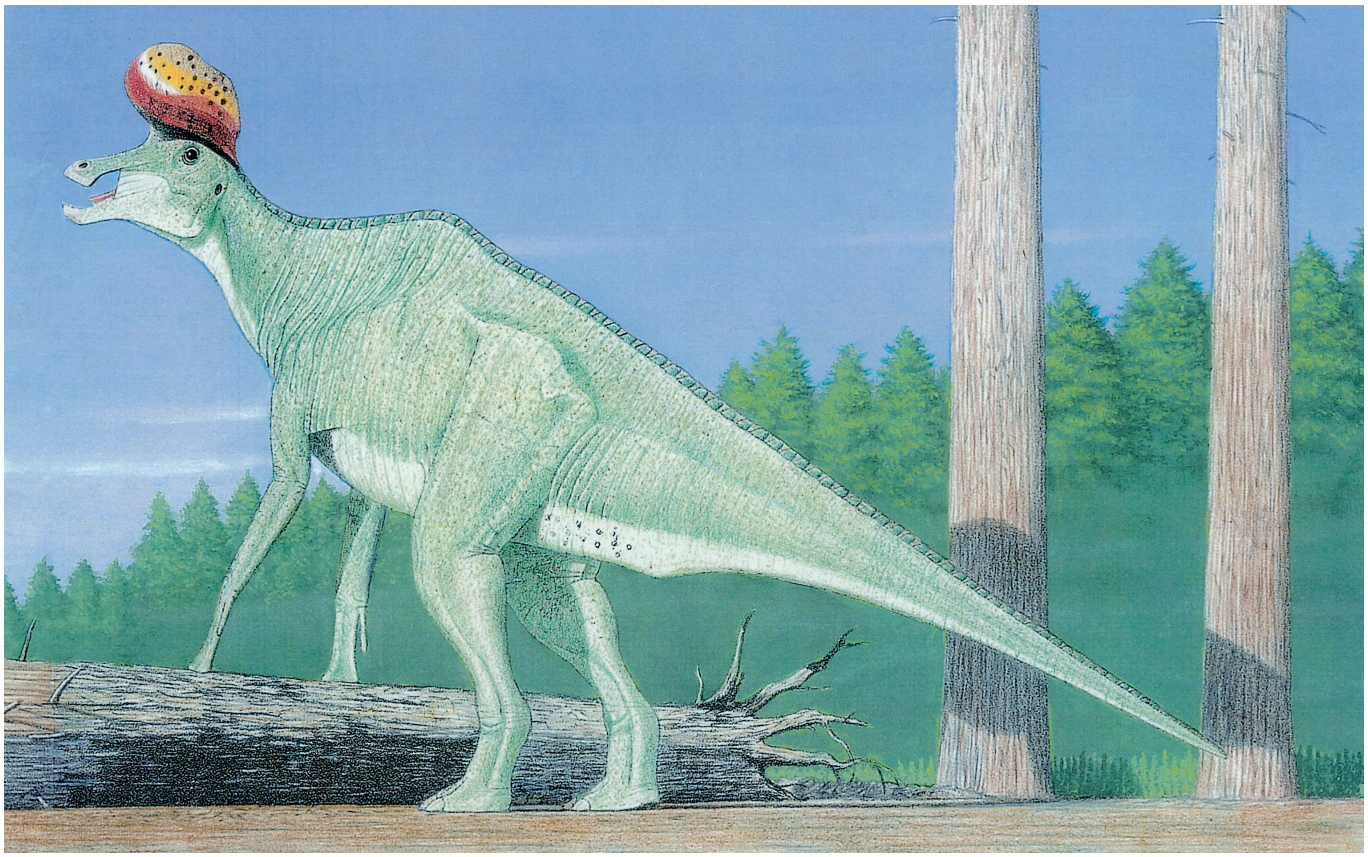


ANATOMICAL CHARACTERISTICS Large, hatchet-shaped crest atop back of head.
AGE Late Cretaceous, early late and middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; middle to upper Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES Fossils with largest crests may be males.

Hypacrosaurus (*Lambeosaurus*) *magnicristatus*

— 7 m (23 ft) TL, 2.6 tonnes
FOSSIL REMAINS A few skulls, part of skeleton.
ANATOMICAL CHARACTERISTICS Extremely large, oblong crest atop back of head.
AGE Late Cretaceous, middle late Campanian.
DISTRIBUTION AND FORMATION/S Alberta; uppermost Dinosaur Park.
HABITAT/S Well-watered, forested floodplain with coastal swamps and marshes, cool winters.
NOTES May be the direct descendant of *H. lambei*.

Hypacrosaurus (*Lambeosaurus*) *magnicristatus*



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